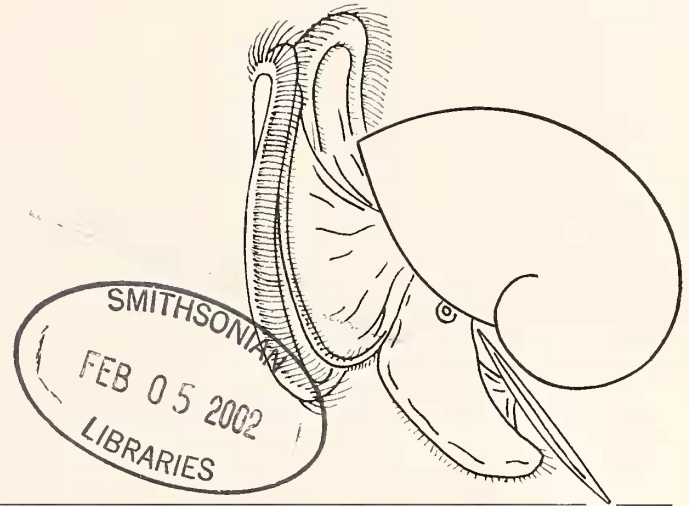


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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Northeastern Pacific Sacoglossan Opisthobranchs: Natural History Review, Bibliography, and Prospectus

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Abstract. The species richness and geographic ranges of the sacoglossan (synonym: ascoglossan) opisthobranch fauna have been well characterized for northeastern Pacific shores, particularly in the Californian province, but the natural history and ecology of these gastropods have been comparatively less well studied. Over half of the described sacoglossan genera and approximately two-thirds of the families are represented on northeastern Pacific shores. At least 25 species of sacoglossans occur: eighteen species are known stenophagous herbivores, and one feeds on opisthobranch eggs. Eight species occur on cold-temperate northeastern Pacific shores, 19 species inhabit the Gulf of California and warm-temperate to tropical Pacific shores, and four species occur in the Aleutian, Oregonian, Californian, and Panamic provinces. Five of the species have been studied appreciably more than the others: *Elysia hedgpethi* (Marcus, 1961), *Alderia modesta* (Lovén, 1844), *Placida dendritica* (Alder & Hancock, 1843), *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905), and *Stiliger fuscovittatus* Lance, 1962. The paucity of study on other species is not necessarily due to low abundance. This natural history review of the regional sacoglossan fauna synthesizes the scattered literature about the stenophagous gastropods and highlights the major gaps that malacologists should seek to fill in the study of this highly specialized order. Future research should focus more on the autecology, population ecology, and community ecology of sacoglossans. Recent advances in isotope analysis, fluorometry, larval culturing, and molecular techniques provide challenging opportunities to enhance our understanding of sacoglossan biology.

INTRODUCTION

Sacoglossan (synonym: ascoglossan) opisthobranchs are small sea slugs that are suctorial feeders on marine algae, seagrass, diatoms, and opisthobranch eggs (Williams & Walker, 1999). Our knowledge of the northeastern Pacific sacoglossan fauna is quite recent, with a rapid proliferation in species recognized since 1960 (Figure 1). Many of the northeastern Pacific species that are broadly distributed were first described in other parts of the world (Figure 1) and then subsequently recorded as present on northeastern Pacific shores. The rate of species discovery is still high (e.g., Farmer, 1996; Lance, 1998; J. Goddard, personal communication, 2000; Valdés & Camacho-García, 2000). Whether such finds are due to (1) locating easily overlooked species (i.e., problem of omission), (2) previous lack of study (Lee & Foster, 1985), or (3) establishment of introduced species is not entirely clear. Most of the recent discoveries have been in the Panamic province.

Beeman & Williams (1980:309) astutely noted: "Studies of California opisthobranchs to date have been mainly taxonomic and distributional in nature." In addition, not only is classification within the order Sacoglossa highly unstable (Roller, 1970a; Marcus, 1982; Gascoigne, 1985; Jensen, 1996; Burn, 1998; Williams & Walker, 1999; Mikkelsen, 1998) but also the proper name of the order

and several species are controversial (Keen, 1973; Jensen, 1991; K. B. Clark, personal communication, 1986; Marshall & Willan, 1999). There remains a continued division in usage of the terms Ascoglossa vs. Sacoglossa; the controversy has been exacerbated by numerous prominent authors switching terms between papers and, in at least one case, within papers. After extensive discussions with taxonomists, I now change from my past use of Ascoglossa to Sacoglossa. Despite the taxonomic and nomenclatural issues, however, in the last two decades, our knowledge of northeastern Pacific species has substantially matured with studies on the ecology, ecophysiology, and reproductive biology of sacoglossan slugs.

The order has recently been reviewed from a number of different perspectives: feeding ecology (Williams & Walker, 1999), kleptoplasty (Clark et al., 1990; Clark, 1992; Williams & Walker, 1999), population ecology (Clark & DeFreese, 1987), and taxonomy (Jensen 1996, 1997; Mikkelsen, 1998). For many geographic regions, there are admirable syntheses of the sacoglossan fauna, their biology and ecology. The present paper (1) synthesizes the existing, broadly scattered details, (2) highlights an unpublished M.A. thesis (Case, 1972) on *Stiliger fuscovittatus* cited only once (by Behrens, 1980) in the past three decades, and (3) evaluates our present understanding of the northeastern Pacific sacoglossan assemblage. Because of these objectives, some of the topics in this

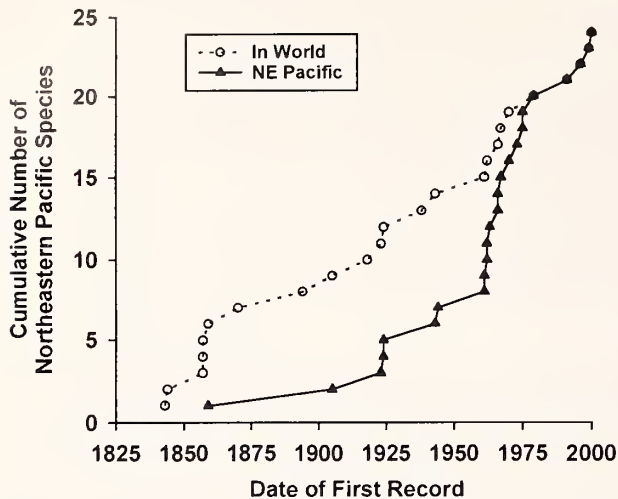


Figure 1. Temporal pattern of species discovery and/or description for northeastern Pacific sacoglossans. Open circles represent first records, for other parts of the world, of species now known from northeastern Pacific shores; closed triangles represent first records of northeastern Pacific species on these shores. Data based on Cockerell & Eliot, 1905; Ageršborg, 1923; MacFarland, 1924, 1966; O'Donoghue, 1924; Pilsbry & Olsson, 1943; Sowell, 1949; Hand, 1955; Marcus, 1961; Keen & Smith, 1961; Lance, 1962; Marcus & Marcus, 1967, 1970a, b; Keen, 1971; Sphon, 1971; Sphon & Mulliner, 1972; Ferreira & Bertsch, 1975; Oakes, 1979; Behrens, 1991a; Valdés & Camacho-García, 2000; J. Goddard, personal communication, 2000.

review (e.g., phenology) are necessarily based on personal communications, observations, or unpublished data by professional colleagues; quantitative descriptions and experimental underpinnings will be (or should be) published in due course. Finally, this review does not attempt to clarify the taxonomic identities of the undescribed species or to resolve issues of problematic species. The primary objective is to provide a cohesive understanding of past work and to provide a focused prospectus for future sacoglossan research.

TAXONOMIC RICHNESS

The number of species, termed "species richness," varies depending on the author and the specific range considered. McDonald (1975) listed seven species for the central California coast, Ricketts et al. (1985:562) mentioned "seven or eight species on our coast" and provided some early references for the Pacific coast, and Beeman & Williams (1980) provided excellent descriptions of two species and briefly mentioned four other species on Californian shores. Farmer (1980) provided comprehensive summaries of nine species for the northeastern Pacific, incorporating the Gulf of California species, and Keen (1971) summarized the species on tropical eastern Pacific shores. Behrens (1991a, b) illustrated and briefly described 12 species and mentioned one other. If these records are

merged, there are at least 25 species (20 described, five undescribed) on northeastern Pacific shores between Alaska and Baja California, including the Gulf of California (Table 1). With increased study of low latitude northeastern Pacific shores (Mexico to northern Ecuador), more species will undoubtedly be discovered.

In terms of higher-level taxonomic diversity, Jensen (1996) listed nine families, 23 genera, and approximately 200 species worldwide in the order Sacoglossa. Based on Jensen's (1996) classification system, there are an estimated 66.7% of the families represented, 60.9% of the genera, and 12.5% of the species in the northeastern Pacific region. Depending on the specific boundaries recognized between biogeographical provinces (Vermeij, 1978; Hartman & Zahary, 1983), the species richness varies (Table 1). There are substantially more sacoglossans known from the Panamic Province (Gulf of California and northeastern Pacific, from Bahía Magdalena south) than from the northern provinces.

GEOGRAPHIC RANGES

Our knowledge of the geographic ranges of these species (Tables 2, 3) is incomplete, owing to gaps in sampling and, in some cases, a lack of sampling outside known ranges. Bertsch (1973:51) noted: "The ranges probably reflect the concentration of study in a few areas as much as the actual ranges of the species." The vast majority of reports on northeastern Pacific sacoglossans are listed as "range extensions," implicitly indicating increases in known ranges. Such records should not be considered "range extensions" in the strictest sense because there is no evidence that species are modifying their ranges but rather our knowledge of the ranges is changing (Clark, 1997); malacological terminology is presently inconsistent with other fields (e.g., population ecology and invasion biology) and thus subject to confusion.

All of the species found on cold-temperate and boreal shores (Oregonian and Aleutian Provinces) are also found in the Californian Province; four of these species also occur in the Gulf of California (Panamic Province) (Table 1). With the possible exception of the seemingly uncommon *Aplysiopsis oliviae*, *Placida* sp. 1, and *Olea hansineensis*, most of the other Pacific coast species are widely distributed in the northeastern Pacific. The southern extent of the ranges of species found in the Gulf of California is generally not well known; this undoubtedly reflects the paucity of opisthobranch studies on low-latitude, northeastern Pacific shores.

Three species have curious and perhaps questionable ranges: *Ercolania fuscata*, *E. boodleae*, and *Stiliger fuscovittatus*. (1) *Ercolania fuscata* occurs on northwestern Atlantic shores (Clark, 1975), the tip of South America, possibly southeastern Australia (Thompson, 1973; but see Jensen & Clark, 1983), and the Gulf of California; as Ferreira & Bertsch (1975) emphasized, this distribution

Table 1

Sacoglossan opisthobranchs on northeastern Pacific shores. Classification based on Jensen (1996). *Cylindrobulla californica* Hamatani, 1971, is not included because Jensen (1996) excluded the family Cylindrobullidae from the order Sacoglossa (but see Mikkelsen, 1998). Provinces based on Vermeij (1978) and Hartman & Zahary (1983).

Species	Aleutian Province	Oregonian Province	Californian Province	Panamic Province
SUBORDER OXYNOACEA (SHELLED SLUGS)				
FAMILY OXYNOIDAE (REDUCED SHELL SLUGS)				
<i>Oxynoe panamensis</i> Pilsbry & Olsson, 1943				X
<i>Lobiger souverbii</i> Fischer, 1856				X
FAMILY JULIIDAE (BIVALVED SLUGS)				
<i>Berthelinia chloris</i> (Dall, 1918)			X	X
<i>Julia thecaplora</i> (Carpenter, 1857) ¹				X
SUBORDER PLAKOBRANCHACEA				
SUPERFAMILY PLAKOBRANCHIOIDEA (PARAPODIA-BEARING SLUGS)				
FAMILY PLAKOBRANCHIIDAE				
<i>Elysia hedgpethi</i> Marcus, 1961	X?	X	X	X
<i>Elysia</i> sp. 1 of Behrens (1991)			X?	X?
<i>Elysia diomedea</i> (Bergh, 1894) ²				X
<i>Elysia oerstedii</i> Mörch, 1859				X
<i>Elysia vreelandae</i> Marcus & Marcus, 1970				X
SUPERFAMILY LIMAPONTIOIDEA (CERATA-BEARING SLUGS)				
FAMILY POLYBRANCHIIDAE				
<i>Polybranchia viridis</i> (Deshayes, 1857) ³				X
<i>Cyerce ortei</i> Valdés & Camacho-García, 2000				X
FAMILY HERMAEIIDAE				
<i>Aplysiopsis enteromorphae</i> (Cockerell & Eliot, 1905) ⁴	X	X	X	X
<i>Aplysiopsis oliviae</i> (MacFarland, 1966)	X?	X	X	
undescribed species ⁵			X	
<i>Hermaea vancouverensis</i> O'Donoghue, 1924	X	X	X	
<i>Hermaea hillae</i> Marcus & Marcus, 1967				X
FAMILY LIMAPONTIIDAE				
<i>Alderia modesta</i> (Lovén, 1844)	X	X	X	
<i>Ercolania boodleae</i> (Baba, 1938)			X	X
<i>Ercolania fuscata</i> (Gould, 1870)				X
<i>Olea hansineensis</i> Agersborg, 1923	X	X	X	
<i>Placida dendritica</i> (Alder & Hancock, 1843)	X	X	X	X
<i>Placida</i> sp. 1 of Behrens (1991)			X	
<i>Stiliger fuscovittatus</i> Lance, 1962	X	X	X	X
<i>Stiliger</i> sp. ⁶				X
<i>Stiliger</i> sp. ⁷				X
Total Number of Species	6–8	8	12–13	18–19

¹ (Synonym: *J. equatorialis* Pilsbry & Olsson, 1944) based on Williams & Gosliner (1973).

² Name change by Gosliner (1995).

³ Synonym: *Phyllobranchillus viridis* (Deshayes, 1857).

⁴ Not *enteromorphae* as listed in MacFarland, 1966 (see Marcus & Marcus, 1967; Behrens, 1991a).

⁵ Found by M. Chamberlain in southern California (D. Behrens, personal communication, 2000).

⁶ Found by Lance & Farmer in the Gulf of California on *Codium magnum* (Farmer, 1996; Lance, 1998; D. Behrens, personal communication, 2000).

⁷ Found by Jeff Goddard in the Gulf of California on *C. fragile* (J. Goddard, personal communication, 2000).

? Reflects the uncertainty in dividing lines between biogeographic provinces (see Hartman & Zahary, 1983).

is rather unusual. It may indicate the species' introduction along historical trade routes (Ferreira & Bertsch, 1975) or cryptic species (Burn, 1998; Ellis, 1999; Burn, personal communication to Ellis, 2000). (2) *Ercolania boodleae*

is common on Japanese shores (Baba, 1938; Usuki, 1977; Trowbridge, personal observations) but was only recently reported in the Gulf of California (Farmer, 1980; Behrens, 1991a). This pattern is symptomatic of a recent species

Table 2

Distribution of common sacoglossans on northeastern Pacific shores

Species	Locations	References
<i>Elysia hedgpethi</i>	<p>Alaska: no records</p> <p>British Columbia: Gibraltar Is., Diana Is., Bordelais Islets, Brady's Beach, Grapper Inlet near Bamfield, Vancouver Is.; Brentwood Bay, Vancouver Is.</p> <p>Washington: San Juan Is.</p> <p>Oregon: Boiler Bay & Seal Rock, Lincoln Co.; Coos Bay, Coos Co.</p> <p>California: Tomales Bay Oyster Company mudflats & Richardson Bay, Marin Co.; near Redwood Creek & Port of Redwood City, SF Bay; Pebble Beach, Moss Beach, Park's Point, Pescadero Point, Point Pinos, Monterey Co.; Elkhorn Slough; Shell Beach & Morro Bay, San Luis Obispo Co.; Point Sal, Coal Oil Point, Santa Barbara Yacht Harbor, Carpinteria, Santa Barbara Co.; Flat Rock, Palos Verdes, Los Angeles Co.; La Jolla; Newport Bay, Orange Co.</p> <p>Baja California: Bahía San Quintín, Bahía Tortugas, Bahía de los Angeles, Puertecitos</p> <p>Sonora: Bahía de San Carlos</p>	<p>Lance (1961, 1966), Marcus (1961), Steinberg (1963), MacFarland (1966), Farmer (1967), Sphon & Lance (1968), Greene (1970a, b, c), Roller (1970b), Goddard (1973, 1984), Green & Muscatine (1972), Gosliner & Williams (1973), Williams & Gosliner (1973), Behrens & Tuel (1977), Millen (1980), T. Gosliner in Behrens (1991a), Lance (1998), C. Trowbridge (unpublished data)</p>
<i>Alderia modesta</i>	<p>Alaska: Cordova, Prince William Sound*</p> <p>British Columbia: Neroutsos Inlet near Port Alice, Ladysmith, Pachena Estuary, Louie Bay, Esperanza Inlet, Vancouver Is.</p> <p>Washington: Garrison Bay & False Bay, San Juan Island</p> <p>Oregon: Coos Bay and Charleston, Coos Co.; Yaquina Bay, Lincoln Co.</p> <p>California: Freshwater Slough, Park Street Slough, & Park Street marsh in Arcata Bay, Humboldt Co.; Bodega Bay, Schooner Bay, Drake's Estero, Marin Co.; Bay Farm Is., Alameda Co.; San Francisco Bay; Elkhorn Slough, Monterey Bay; Newport Bay, Orange Co.; San Elijo estuary, Kendall-Frost Marine Reserve and Northern Wildlife Preserve, San Diego River Flood Control Channel, & Mission Bay, San Diego Co.</p> <p>Baja California: San Quintín Bay</p> <p>Other: North Atlantic shores</p>	<p>Hand (1955), Hand & Steinberg (1955), Steinberg (1963), Gosliner & Williams (1973), Williams & Gosliner (1973), Belcik (1975), Thompson (1976), McLean (1978), S. V. Millen (1980, personal communication, 2000), J. Goddard (1984, personal communication, 2000), Jaeckle (1984), Trowbridge (1993c), Lance (1996), Krug (1998b), Krug & Manzi (1999), W. Farmer (personal communication, 1999)</p>
<i>Aplysiopsis enteromorphae</i>	<p>Alaska: Cutter Rock, Ketchikan</p> <p>British Columbia: Crescent Beach; Gambier Is.; Grappler Inlet, Bamfield, & Esperanza Inlet, Vancouver Is.</p> <p>Washington: Argyll Lagoon, Garrison Bay, Wescott Bay, & Mitchell Bay, San Juan Is.; Kayostla Beach</p> <p>Oregon: Boiler Bay & Seal Rock, Lincoln Co.; Neptune Beach & Strawberry Hill, Lance Co.; South Cove, Good Witch Cove, & South Slough, Coos Co.</p> <p>California: Omenoku Pt. & Punta Gorda, Humboldt Co.; Bolinas, Tomales Bay, Bodega Bay; Drake's Estero, Marin Co.; Duxbury Reef, Marin Co.; Scott Creek, Santa Cruz Co.; Elkhorn Slough, Monterey Bay; Cayucos, Hazard Canyon, & Shell Beach, San Luis Obispo Co.; Leo Cabrillo Beach State Park, Los Angeles Co.; Point Sal, Santa Barbara Co.; San Diego; La Jolla Bay, Newport Bay, Orange Co.; Dead Man's Bay, San Pedro</p> <p>Baja California: Bahía de los Angeles, Bahía San Quintín</p> <p>Sonora: Bahía de San Carlos</p>	<p>Cockerell & Eliot (1905), Connor (1961), Lance (1961, 1998), Marcus (1961), Steinberg (1963), MacFarland (1966), Sphon & Lance (1968), Roller & Long (1969), Gosliner & Williams (1970, 1973), Greene (1970a), Williams & Gosliner (1973), Belcik (1975), S. V. Millen (1980, 1989, personal communication, 2000), J. Goddard (1984, 1987, personal communication, 2000), Jaeckle (1984), Behrens (1991a) Trowbridge (1993a, d, personal observations), Goddard et al. (1997), Lance (1998)</p>
<i>Hermaea vancouverensis</i>	<p>Alaska: Humboldt Harbor, Shumagin Islands; Spruce Cape, Kodiak Is.; Cutter Rock & Blank Is., Ketchikan</p> <p>British Columbia: Port Hardy & Newcastle Is., Vancouver Is.; Saturna Is. & Flat Top Is.</p> <p>Washington: Kayostla Beach</p> <p>Oregon: Boiler Bay & Seal Rock, Lincoln Co.; North Cove, Coos Co.</p> <p>California: Bodega Harbor & Coleman State Beach, Sonoma Co.; Duxbury Reef, Marin Co.</p> <p>Baja California: No records</p>	<p>O'Donoghue (1924), Sowell (1949)***, Steinberg (1963), Williams & Gosliner (1973), S. V. Millen (1980, 1983, personal communication, 2000), Goddard (1984), Foster (1987), T. Gosliner in Behrens (1991a), Goddard et al. (1997), Trowbridge (personal observations)</p>

Table 2
Continued

Species	Locations	References
<i>Placida dendritica</i>	<p>Alaska: Bertha Bay, Chichagof Is.</p> <p>B.C.: Triangle Is., Diana Is., Grappler Inlet, Brady's Beach, Port Renfrew, Bamfield, Vancouver Is.; Mills Bay near Victoria</p> <p>Washington: Kayostla Beach; Cattle Point, San Juan Island</p> <p>Oregon: Boiler Bay, Yaquina Head & Seal Rock, Lincoln Co.; Strawberry Hill, Lane Co.; South Cove, Good Witch Cove, & Squaw Is., Coos Co.; S.H. Boardman State Park, Curry Co.</p> <p>California: Palmer's Pt. & Trinidad Bay, Humboldt Co.; Bodega Head, Sonoma Co.; Duxbury Reef, Marin Co.; Richardson Bay, Marin Co.; Fort Barry Docks, SF Bay; Punta Gorda, Humboldt Co.; Carmel Bay, Park's Pt., Pescadero Point, Point Pinos, & Cypress Point, Monterey Co.; Shell Beach & Morro Bay, Pismo Beach, San Luis Obispo Co.; Flat Rock, Palos Verdes, Los Angeles Co.; Newport Beach and Newport Bay, Orange Co.</p> <p>Baja California: Isla San Benito; Bahía San Quintín, Bahía de los Angeles</p> <p>Sonora: Bahía de San Carlos</p> <p>Other: Japan, north Atlantic, Australasia, South Africa***</p>	<p>Sowell (1949)**; MacFarland (1966), Long (1969), Gosliner & Williams (1970), Greene (1970a), Marcus & Marcus (1970a), Roller (1970b), Greene & Muscatine (1972), Goddard (1973, 1984, 1987, 1990), McLean (1976), Williams & Gosliner (1973), Lambert (1976), Thompson (1976), S. V. Millen (1980, personal communication, 2000), Jaeckle (1984), Gosliner (1987), Behrens (1991a, 1998), Trowbridge (1991a, b, 1995, 1998a, b, 1999, unpublished data), Ichikawa (1993) Goddard et al. (1997), Lance (1998), O'Clair & O'Clair (1998)</p>
<i>Stiliger fuscovittatus</i>	<p>Alaska: Cutter Rock, Ketchikan</p> <p>B.C.: Flat Top Islands (Saturina & Bath); Porlier Pass near Galiano Is.; Stubbs Is. near Telegraph Cove, & Sooke Harbour, Vancouver Is.</p> <p>Washington: San Juan Island</p> <p>Oregon: Seal Rock, Lincoln Co.; Isthmus Slough, Coos Bay, Coos Co.</p> <p>California: Arcata Bay & Humboldt Bay, Humboldt Co.; SF Yacht Harbor, Fort Barry, Sausalito, Marin Co.; Morro Bay Docks & Shell Beach, San Luis Obispo Co.; San Diego & Mission Bays</p> <p>Baja California: Bahía de los Angeles</p> <p>Other: Sebastian Inlet Jetty & Indian River Lagoon at Titusville, Florida</p>	<p>Lance (1962, 1966), Steinberg (1963), Roller & Long (1969), Gosliner & Williams (1970), Case (1972), Williams & Gosliner (1973), S. V. Millen (1980, 1989, personal communication, 2000), Jensen & Clark (1983), Jaeckle (1984), Clark & DeFreese (1987), Trowbridge (1994, unpublished data), Clark (1995), J. Goddard (personal communication, 2000)</p>
<i>Olea hansineensis</i>	<p>Alaska: Cordova, Prince William Sound*</p> <p>British Columbia: Tuwanek Pt., Sechelt Inlet; Sooke Harbour & Tofino, Vancouver Is.</p> <p>Washington: Jaekle's Lagoon & Garrison Bay, San Juan Is. & Brown Is. & Parks Bay, Shaw Is.</p> <p>Oregon: No reports</p> <p>California: San Clemente Is.</p>	<p>Agersborg (1923), Gonor (1961), Steinberg (1963), Hurst (1967), Crane (1971), Robilliard (1971), Millen (1980), R. McPeak & D. Mulliner in Behrens (1991a), J. Goddard (personal communication, 2000)</p>

* New records in preparation: J. Goddard (personal communication, 2000).

** Sowell's (1949) record of *Hermaea vancouverensis* probably refers to *Placida dendritica*; this inference is based on the superficial similarity of the two species, the fact that *P. dendritica* was not recognized on northeastern Pacific shores until the 1960's (MacFarland, 1966; Long, 1969), the author's familiarity with the site in Oregon, and perhaps most importantly because the algal host was specified to be the green alga *Bryopsis corticulans*, not the colonial diatom *Isthmia nervosa*. I do not agree with Belcik's (1975) interpretation that the record was *Aplysiopsis enteromorphae* (as *A. smithi*) because of difference in size, color, tidal level, and algal food.

*** May be sibling species (C. Trowbridge, work in progress).

introduction, although additional evidence (e.g., confirming the species identity) is needed to support this hypothesis. (3) The appearance of the northeastern Pacific *Stiliger fuscovittatus* in Indian River Lagoon, Florida (Jensen & Clark, 1983; Clark, 1995) seems also to be due to an anthropogenic introduction, particularly as this species feeds on filamentous red algae (*Polysiphonia*) commonly

growing on ship hulls, floating docks, floats, and other "artificial" surfaces.

Chapman & Carlton (1991) suggested a number of criteria to evaluate whether a species was native or introduced. All three of the above cases may represent cases of introductions, although, based on their criteria, additional information is needed. When Marcus (1961) first

Table 3
Distribution of the less common species of northeastern Pacific sacoglossans

Species	Locations	References
<i>Oxynoe panamensis</i>	Baja California: Espiritu Santo Is., Candelero Bay; near La Paz Other: Bocas Is., Province of Bocas del Toro, Panama	Pilsbry & Olsson (1943), Smith (1961), Doty & Aguilar-Santos (1970), Lewin (1970), Keen (1971), Williams & Gosliner (1973)
<i>Lobiger souverbii</i>	Baja California: Espiritu Santo Is., Candelero Bay; Playa Maria & Isla San Jose, Baja del Sur Nayarit, Mexico: Santa Cruz Galapagos: Flamingo Cove, Floreana Island, Galápagos Islands Other: Indian, Pacific, and Atlantic Oceans	Marcus & Marcus (1967, 1970a), Keen (1971), Sphon (1971), Sphon & Mulliner (1972), Baba (1974), Larson & Bertsch (1974), Jensen (1983), Jensen & Clark (1983), Clark & DeFreese (1987), Gosliner (1987), Ichikawa (1993), Gosliner et al., (1996)
<i>Berthelminia chloris</i>	Baja California: Bahía Ballenas & La Paz; Punta Abreojos; La Paz; Puerto Ballandra Bay; Magdalena Bay; Espiritu Santo Is., Candelero Bay, Gulf of California Galapagos: Flamingo Cove, Floreana Island, Galápagos Islands	Keen & Smith (1961), Smith (1961), Kay (1964), Keen (1971), Sphon & Mulliner (1972), Williams & Gosliner (1973), Behrens (1991a)
<i>Julia thecaphora</i>	Baja California: La Paz Mexico: Sócorro Is. Other: Panama, Colombia, Ecuador, Peru	Pilsbry & Olsson (1944), Keen (1971), Williams & Gosliner (1973)
<i>Elysia vreelandae</i>	Sonora: San Agustín = El Sahuaral	Marcus & Marcus (1970a, b)
<i>Elysia oerstedii</i>	Costa Rica: Puntarenas	Keen (1971)
<i>Elysia</i> sp. 1	Baja California: Magdalena Bay	T. Gosliner in Behrens (1991a)
<i>Elysia diomedea</i>	Baja California: West of Isla Cerralvo; Islas San Francisco, Espiritu Santo, & Cerralvo; Bahía Las Cruces; Bahía Carisalito; Bahía de Concepcion; Bahía de los Angeles; San Marcus Is., Gulf of Calif.; Puerto Lobos; San José Is. Sonora: Puerto Peñasco El Salvador: Pacific coast Other: To Panama Panama: Venado Isl., off Ft. Kobbe; Deale Beach (Ft. Kobbe Beach), Canal Zone	Bergh (1894), MacFarland (1924), Marcus & Marcus (1967), Dushane & Sphon (1968), Trench et al. (1969), Bertsch (1971, 1973), Keen (1971), Bertsch & Smith (1973), Williams & Gosliner (1973), Ireland & Faulkner (1981), Debelius (1996), Bertsch et al. (1998)
<i>Polybranchia viridis</i>	Baja California: Punta Norte, Isla Cerralvo; Rancho Notri Puerto Escondido, Bahía de Palmas, Punta Colorada, Pulmo Reef, Cabo Pulmo Nayarit: Punta Mita Other: Duncan Is. & Flamingo Cove, Floreana Is., Galapagos; Lesser Antilles; Florida; Panama	Marcus & Marcus (1967, 1970a), Sphon & Mulliner (1972), Bertsch & Smith (1973), Ferreira & Bertsch (1975), Clark (1995), Debelius (1996)
<i>Cyerce ortei</i>	Costa Rica: Playa Cabuya, Cabuya, Cóbano, Puntarenas; Estación San Miguel, Reserva Natural Absoluta de Cabo Blanco, Cabuya, Cóbano, Puntarenas; Playa Ocal del Peñon, Santa Teresa, Cóbano, Puntarenas	Valdés & Camacho-García (2000)
<i>Aplysiopsis oliviae</i>	British Columbia: Saltspring Is. & Brentwood Bay, Vancouver Is. California: Duxbury Reef, Marin Co.; Cabrillo Pt. & Pt. Pinos, Monterey Bay; Santa Barbara Channel, Santa Barbara Co.	MacFarland (1966), Lee & Brophy (1969), Gosliner & Williams (1970), Williams & Gosliner (1973), Millen (1980)
<i>Placida</i> sp. 1	California: San Diego Bay	J. Hamann in Behrens (1991a)
<i>Hermaea hillae</i>	Sonora: Puerto Peñasco	Marcus & Marcus (1967)
<i>Stiliger</i> sp.	Baja California: Bahía San Quintín	Farmer (1996), Lance (1998), D. Behrens (personal communication, 2000)
<i>Ercolania boodleae</i>	California: Mission Bay Sonora: Puerto Peñasco Other: Japan	Baba (1938, 1949), Baba & Hamatani (1952, 1970), Usuki (1977), W. Farmer (1980, personal communication, 1999), J. Hamann in Behrens (1991a)

Table 3
Continued

Species	Locations	References
<i>Ercolania fuscata</i>	Sonora: near Puerto Peñasco Other: Florida, northwestern Atlantic	Clark (1975, 1995), Ferreira & Bertsch (1975), Jensen & Clark (1983), Clark & DeFreese (1987), Jensen (1988), references therein

described *Elysia hedgpethi*, he considered whether it might have been introduced, given its occurrence on a mudflat in close proximity to mariculture facilities (Pacific oysters) in Tomales Bay, California; after comparing the species to congeners around the world, he concluded that it was a separate species. Soon after its initial description in 1961, *E. hedgpethi* was reported to be widespread (to the north and south); thus, this species exemplifies an overlooked native that differs from geographically distant endemic species (e.g., from the Japanese *E. japonica*, the European *E. viridis*, etc.).

PREY SPECIES AND FEEDING

Diets

Sacoglossans are traditionally considered to be stenophagous consumers with comparatively specialized host-plant associations (see Williams & Walker, 1999). For 76% of the northeastern Pacific species, the feeding habits have been generally well characterized, at least to the generic level (Table 4). Difficulty or unresolved taxonomy within some algal groups (e.g., *Vaucheria*, *Cladophora*, *Chaetomorpha*) as well as malacologists' inexperience with distinguishing algal species (e.g., *Codium* and *Polysiphonia*) have hindered progress in this area. For *Hermaea hillaie*, *Elysia* sp. 1, *E. oerstedii*, and *Cyerce ortei*, prey species have not been described.

Radulae of many species have been illustrated (O'Donoghue, 1924; Hand & Steinberg, 1955; Gonor, 1961; Lance, 1962; Marcus & Marcus, 1970b; Ferreira & Bertsch, 1975; Gascoigne, 1975; Farmer, 1980; Bleakney, 1989, 1990; Behrens, 1991b; Valdés & Camacho-García, 2000). Jensen (1980, 1993, 1996, 1997) hypothesized that tooth shape is directly related to food type. Jensen's results may assist in determining the diets of the poorly studied species; such extrapolation would be a useful tool for future study of uncommon sacoglossans. Furthermore, Bleakney (1989, 1990) and Jensen (1996, 1997) have reported intraspecific variation in radular tooth morphology in two species on different diets; it would be intriguing to know whether this phenomenon also occurs in *Aplysiopsis enteromorphae*, *Elysia hedgpethi*, and other northeastern Pacific species that feed on two or more genera of algae.

The feeding ecology of northeastern Pacific sacoglossans has been investigated experimentally for only a few species: *Placida dendritica* (Trowbridge, 1991a, b, 1992a, b, 1993b, 1997, 1998a, b), *Elysia hedgpethi* (Trowbridge, unpublished data), *Aplysiopsis enteromorphae* (Gonor, 1961; Trowbridge, 1993a), *Stiliger fuscovittatus* (Case, 1972), *Ercolania fuscata* (on Atlantic shores; Clark, 1975; Jensen, 1983), and *Ercolania boodleae* (on Japanese shores; Usuki, 1977). As Williams & Walker (1999) have emphasized, there is considerable room for improvement in the experimental and statistical rigor of feeding experiments. For example, for feeding preference experiments, some of the needed changes include (1) adequate replication and (2) independence of replicates (individual animals in separate containers making separate and individual choices). For experiments in which groups of animals are maintained on different diets (e.g., Chia & Skeel, 1973), the container or dish is the replicate, not the animals within the dish. For experiments in which groups of animals are placed in a single arena with a pairwise choice of algal species (e.g., Jensen, 1983), the individual slugs are not independent and thus cannot constitute replicates. If experiments involve measuring prey mass loss due to slug herbivory, negative controls should be included in order to measure the endogenous mass loss in the absence of herbivory. Peterson & Renaud (1989) describe the statistical methodology required to test for significant preferences between pairwise choices; multiple-choice experiments are fraught with statistical peril despite their clear biological significance.

Even with the best-studied associations, slug discrimination among, preference of, and performance on congeneric algal species have not been resolved. For example, *Placida dendritica* exhibits distinct feeding preferences among three algal hosts on Oregon shores (*Bryopsis corticulans*, *Codium fragile*, and *C. setchellii*) (Trowbridge, 1991a); on northeastern Pacific shores, there are at least six potential host species, yet there is no information on whether *P. dendritica* consumes *C. ritteri* in Alaska, *C. cuneatum*, *C. hubbsii*, or *C. johnstonei* in southern California, or *C. magnum* and allies in the Gulf of California. Similarly, many authors report that *Stiliger fuscovittatus* consumes *Polysiphonia pacifica*, *Polysiphonia* sp., and *Callithamnion* sp. (Lance, 1962; Stein-

Table 4

Adult diets described for northeastern Pacific sacoglossan opisthobranchs. In many cases, it is unclear if authors are reporting their own observations of diets or merely reiterating previous reports.

Species	Diets	Description of prey	References
<i>Oxynoe panamensis</i>	<i>Caulerpa sertularioides</i> , <i>Halimeda</i>	coenocytic green algae	Doty & Aguilar-Santos (1970), Lewin (1970), Keen (1971)
<i>Lobiger souverbii</i>	(<i>Caulerpa racemosa</i> , <i>C. brachypus</i> , <i>C. paspaloides</i> , <i>C. serrulata</i>)*	coenocytic green algae	Sphon & Mulliner (1972), Baba (1974), Clark & Busacca (1978), Jensen (1983), Clark & DeFreese (1987), Gosliner (1987), Ichikawa (1993)
<i>Berthelina chloris</i>	<i>Caulerpa racemosa</i> , <i>C. sertularioides</i>	coenocytic green algae	Kay (1964), Sphon & Mulliner (1972), Marcus & Marcus (1970a)
<i>Elysia hedgpethi</i>	<i>Codium fragile</i> , <i>C. setchellii</i> , <i>Bryopsis corticulans</i>	coenocytic green algae	MacFarland (1966), Millen (1980), C. Trowbridge (unpublished data)
<i>Elysia diomedea</i>	<i>Padina</i> and perhaps <i>Spyridia</i>	brown algae	Bertsch & Smith (1973)
<i>Elysia vreelandae</i>	<i>Codium</i>	coenocytic green algae	Marcus & Marcus (1970b)
<i>Polybranchia viridis</i>	<i>Caulerpa racemosa</i>	coenocytic green algae	Bertsch & Smith (1973)
<i>Aplysiopsis enteromorphae</i>	<i>Cladophora columbiana</i> , <i>C. trichotoma</i> , <i>Chaetomorpha linum</i> , <i>C. aerea</i> , <i>Urospora</i> , <i>Rhizoclonium</i>	filamentous green algae	Gonor (1961), Greene (1968, 1970a), Millen (1980), Goddard (1984, 1987), Trowbridge (1993a), Lance (1998)
<i>Aplysiopsis oliviae</i>	<i>Griffithsia pacifica</i> , <i>Polysiphonia hendryi</i>	red algae	Millen (1980)
<i>Hermaea vancouverensis</i>	<i>Isthmia nervosa</i>	diatom	Williams & Gosliner (1973), Foster (1987)
<i>Alderia modesta</i>	<i>Vaucheria</i> spp.	xanthophyte	Hand (1955), Hand & Steinberg (1955), Millen (1980)
<i>Olea hansineensis</i>	<i>Precnthona</i> , <i>Haminoea</i> , <i>Melanochlamys</i> , <i>Gastropteron</i> , <i>Archidoris</i> , <i>Hermisenda</i> , <i>Dendronotus</i>	opisthobranch eggs	Hurst (1967), Crane (1971), Robilliard (1971), Millen (1980)
<i>Placida dendritica</i>	<i>Codium fragile</i> , <i>C. setchellii</i> , <i>Bryopsis corticulans</i> , (<i>Derbesia</i> , <i>Codium</i> spp., <i>Caulerpa lentillifera</i> , or <i>Halimeda cuneata</i>)*	coenocytic green algae	MacFarland (1966), Long (1969), Greene (1970c), Roller (1970b), Williams & Gosliner (1973), Lambert (1976), McLean (1976), Millen (1980), Gosliner (1987), Bleakney (1989, 1990), Behrens (1991a), Trowbridge (1991a, b, 1992a, b), Ichikawa (1993)
<i>Placida</i> sp. 1	<i>Cladophora</i> **	filamentous green algae	Oakes (1979)
<i>Stiliger fuscovittatus</i>	<i>Polysiphonia pacifica</i> , <i>Polysiphonia brodiaei</i> , <i>P. paniculata</i> , and <i>Callithamnion</i> sp.***	red algae	Lance (1962), Steinberg (1963), Beeman & Williams (1970), Case (1972), Clark & Busacca (1978)
<i>Stiliger</i> sp.	<i>Codium magnum</i>	coenocytic green algae	Farmer (1996), Lance (1998)
<i>Stiliger</i> sp.	<i>Codium fragile</i>	coenocytic green algae	J. Goddard (personal communication, 2000)
<i>Ercolania boodlea</i>	<i>Chaetomorpha</i> , <i>Cladophora</i> (<i>Ulva</i> , <i>Enteromorpha</i> , <i>Boodlea</i>)*	filamentous green algae	Baba (1938, 1949), Baba & Hamantani (1952, 1970), Usuki (1977), photograph in Behrens (1991a)
<i>Ercolania fuscata</i>	<i>Cladophora</i> , <i>Chaetomorpha</i> , (<i>Cladophoropsis</i> , <i>Bryopsis</i>)*	filamentous green algae	Clark (1975), Jensen (1983), Clark & DeFreese (1987)

* Algae in brackets are on Japanese shores (Baba, 1938, 1949, 1974; Ichikawa, 1993), northwestern Atlantic shores (e.g., Clark, 1975; Jensen, 1983; Jensen & Clark, 1983; Clark & Busacca, 1978), or South African shores (Gosliner, 1987).

** Collected on alga; not sure what it feeds on (D. Behrens, personal communication, 2000) but see Oakes (1979).

*** Not *Microcladia coulteri* mentioned by Beeman & Williams (1970); the confusion undoubtedly arose as the slug species was photographed on *M. coulteri* in the original species description (Lance, 1962) and in Behrens (1991a).

berg, 1963; Beeman & Williams, 1980). Case (1972), however, reported that *S. fuscovittatus* ate three species in San Francisco Bay: *P. pacifica*, *P. brodiaei*, and *P. paniculata*. Given that there are about 17 species of *Polysiphonia* reported for California, many of which have recognized varieties, it would be intriguing to know how many algal species actually can be used as host species for *S. fuscovittatus*. Clark (1994, 1995) hypothesized that sacoglossans are particularly vulnerable to environmental or anthropogenic changes, owing to their apparent dependence on specific host plants. Little is known, however, to what extent other algal species can serve as alternate hosts.

A related issue is whether sacoglossans are stenophagous at the local scale but more polyphagous at the regional scale (see discussion by Fox & Morrow, 1981). This could occur if diet specificity is affected by developmental processes (e.g., induction of specific digestive enzymes or tooth morphology by initial diet). Recent work on a European sacoglossan (Trowbridge & Todd, 1998, 2001) indicates that the algal substratum used to induce larval metamorphosis does affect subsequent feeding preferences of post-metamorphic juveniles. The role of genetic variation in feeding preferences has not yet been examined but may contribute to regional variability in diet; extensive work on suctorial insects, the terrestrial analog of sacoglossans, has demonstrated the importance of genetic mechanisms (see, for example, Trowbridge, 1991a; Trowbridge & Todd, 2001).

Particularly surprising is the paucity of information about how native sacoglossans have responded to introduced potential hosts. For example, although the invasive pest alga *C. fragile* ssp. *tomentosoides* has occurred in San Francisco Bay, California since 1973 (Silva, 1979), and the alga is a potential host for *Placida dendritica* and *Elysia hedgpethi*, there have been no published studies on temporal changes in host-plant use with the appearance of a new host plant on Pacific shores. The issue has been investigated on northwestern Atlantic shores (Clark & Franz, 1969; Clark, 1975; Bleakney, 1996), northeastern Atlantic shores (Trowbridge & Todd, 1998, 2001), and Australasian shores (Trowbridge, 1995, 1999). Analogous work is being done on Australian and Mediterranean shores with sacoglossans attacking introduced species of *Caulerpa*. With the appearance of *Caulerpa taxifolia* ("killer algae") in San Diego, California, such issues become more pressing.

Finally, a few cases of slug-algal associations have been reported which may not be related to feeding. For example, *Elysia hedgpethi* is often found either crawling on or depositing its egg masses on the green alga *Ulva* or red foliose algae (e.g., Steinberg, 1963; MacFarland, 1966; Behrens & Tuel, 1977). *Aplysiopsis enteromorphae* in high tidepools selects *Mastocarpus papillatus* (= *Gigartina papillata*) for this purpose (C. Trowbridge, personal observation), and conspecifics on mudflats often oc-

cur on the green alga *Enteromorpha* (which the slugs do not eat, despite the slug's species name; Gonor, 1961). Although the significance of the following has not been generally investigated, Case (1972) reported that eggs of *Stiliger fuscovittatus* develop faster when deposited on algal hosts than on glass or loose in seawater. I have also observed slugs clustering on or under non-food macroalgae, presumably to ameliorate desiccation stress during daytime low tides. Finally, experimental work on a European sacoglossan has demonstrated that larvae will settle and metamorphose on non-host species (Trowbridge & Todd, 2001), and Krug (2001) has documented an analogous situation with larval *Alderia modesta* in California. While we must be careful in inferring trophic associations from the presence of a slug on a particular alga (as emphasized by Jensen), field observations of slugs on algae are important and may reflect either trophic associations or previously overlooked, non-trophic aspects of slug biology.

Foraging and Feeding Behavior

Comparisons of the sacoglossan literature to that of generalist gastropods and other herbivorous invertebrates (e.g., Hawkins & Hartnoll, 1983) reveal major gaps of study in the sacoglossan field; Williams & Walker (1999) noted gaps as well. At least six key issues have not been explored for northeastern Pacific sacoglossans:

- (1) Frequency of feeding.
- (2) Presence of temporal feeding patterns.
- (3) Extent of long and short-range chemoreception of prey species.
- (4) Importance of algal physiological condition.
- (5) Ecological effects of slug grazing.
- (6) Energetics of slugs.

With respect to the first topic, observational data are meager, and quantitative data are lacking (Williams & Walker, 1999). The northeastern Pacific *Olea lansineensis* reportedly feeds periodically a few times per day (Crane, 1971), whereas *Elysia hedgpethi* feeds continuously (Greene, 1970c). Graves et al. (1979) reported that the digestive lumina of *Alderia modesta* contain chloroplasts, suggesting that the species feeds "regularly," whereas the kleptoplastic *Elysia chlorotica* feeds only periodically. The frequency of feeding is difficult to observe directly, given the small size of sacoglossans and the ventral location of the mouth.

Regarding temporal patterns, two-day feeding experiments with *Placida dendritica*, *Elysia hedgpethi*, and *Aplysiopsis enteromorphae* indicate no clear distinctive tidal or diurnal periodicity (see Trowbridge, 1991a, b, 1993a, b). Weaver & Clark (1981) reported that Atlantic species with functional chloroplasts oriented toward light, whereas aposymbiotic species avoided light. If this pattern were general, then most northeastern Pacific species

Table 5

Type of chloroplast retention of northeastern Pacific sacoglossans. Species with melanic pigmentation generally lack functional kleptoplasty (Clark et al., 1990).

Species	Melanic pigment	Type of kleptoplasty	References
<i>Oxynoe panamensis</i>	—	short-term non-functional retention	Muscatine & Greene (1973), Clark et al. (1990)
<i>Lobiger souverbii</i>	—	short-term non-functional retention	Clark et al. (1990)
<i>Berthelinia chloris</i>	—	short-term non-functional retention	Muscatine & Greene (1973), Clark et al. (1990)
<i>Julia thecaphora</i>	—	short-term non-functional retention	Clark et al. (1990)
<i>Elysia hedgpethi</i>	—	short-term (< 12 h) functional retention	Greene (1970a, b, c), Greene & Muscatine (1972)
<i>Elysia diomedea</i>	—	functional retention	Trench et al. (1969)
<i>Polybranchia viridis</i>	—	short-term non-functional retention	Clark, personal observations in Clark et al. (1990)
<i>Aplysiopsis enteromorphae</i>	+	short-term non-functional retention	Clark et al. (1990); but see Greene (1970a)
<i>Alderia modesta</i>	—	short-term (< 12 hr) functional retention	Graves et al. (1979), Clark et al. (1990)
<i>Placida dendritica</i>	—	intermediate non-functional retention	McLean (1976), Greene & Muscatine (1972), Clark et al. (1990)
<i>Ercolania fuscata</i>	+	no retention	Clark et al. (1990)

(Table 5) should avoid light or perhaps be nocturnal because of the general lack of functional kleptoplasty. Rigorous experiments and field observations are needed to address this temporal-pattern hypothesis. Although numerous studies assert sacoglossan crypsis and susceptibility to predators, there is a noteworthy absence of quantitative data documenting temporal patterns of activity patterns for northeastern Pacific slugs. Similarly, for most intertidal species, it is not known whether slugs feed during emergence and/or submergence. *Elysia diomedea* moves around actively during the day at rates up to 9.5 cm minute⁻¹ and feeds underwater (Marcus & Marcus, 1967; Bertsch & Smith, 1973). *Alderia modesta* moves around on *Vancheria* mats in the daytime (Trowbridge, 1994), although night observations have never been made. Slugs burrow into the algal mats with increased emergence time, particularly on warm or bright days (Trowbridge, 1994), and thus appear to be active primarily during submergence.

The role of chemoreception in host-plant location for post-metamorphic slugs and for competent veliger larvae has not been explored for northeastern Pacific species (but see Krug & Zimmer, 2000). Jensen (1982, 1988) investigated the mode of chemoreception for tropical species in Florida, but research on Pacific shores is needed. Limited observations suggest that *Olea hansineensis* moves "randomly" across mudflats, locating opisthobranch eggs by chance or perhaps by extremely short-ranged perception (Crane, 1971). In contrast, the extremely rapid recruitment of *Placida dendritica* to algal transplants on Oregon shores (Trowbridge, 1992a, b, 1998b)

suggests that larvae have extremely acute long-distance host detection. Den Hartog (1959) reported that *Alderia modesta* reacted to chemical stimuli from algal food; in contrast, *Aplysiopsis enteromorphae* and *Ercolania boodlea* do not react when presented with cell sap of their algal food (Gonor, 1961; Usuki, 1977), indicative of little, if any, chemoreception. *Ercolania fuscata* exhibited a positive response to algal homogenates (Jensen, 1988), although the nature of the compounds was not identified nor was the effective distance defined over which the cues operated.

Until we know the nature of the cues inducing larval metamorphosis of sacoglossans and the degree of specificity of such cues (see Krug, 2001; Krug & Manzi, 1999; Krug & Zimmer, 2000a, b), we will not be able to understand fully the extent of the stenophagy of the slugs. For example, it has traditionally been assumed that larval metamorphosis of sacoglossans (and for most opisthobranchs) occurs only in response to prey species of the adults. In laboratory experiments with the Atlantic *Elysia viridis*, however, competent larvae metamorphosed on a variety of macroalgae species, including host and non-host algae (Trowbridge & Todd, 1998, 2001). Furthermore, for northeastern Pacific *Alderia modesta*, some larvae in every lecithotrophic clutch metamorphose immediately with no inductive cue, whereas the remaining larvae delay metamorphosis indefinitely until either encountering *Vancheria*, or dying (Krug, 2001, personal communication, 2000).

In terrestrial herbivore-plant interactions, the nitrogen status, stress level, and physiological condition of the

plants strongly affect herbivory of stenophagous and polyphagous herbivores (reviewed by Trowbridge, 1998b); in marine associations, however, comparable information is generally lacking for intraspecific variation in herbivory. The two notable exceptions are experimental studies with *Placida dendritica*. First, Trowbridge (1998b) reported that desiccation-stressed algal hosts were attacked more frequently by *P. dendritica* than were unstressed thalli on Oregon (and New Zealand) shores. The basis was not improved food quality or attractiveness to adult slugs; the apparent mechanism was that exudates from stressed algal hosts induced higher rates of settlement and metamorphosis to competent larvae than did exudates from unstressed hosts (Trowbridge, 1998b). Second, Trowbridge (1991a) found that adult slugs exhibited no preferences between mechanically damaged and undamaged algal tissue but did grow faster on algae damaged by grazing conspecifics.

Williams & Walker (1999) reviewed the ecological effect of slug herbivory on algal populations. Presumably, species that do not retain functional chloroplasts cause more grazing damage than species that supplement their nutrition with endosymbiosis or kleptoplasty. To what extent do northeastern Pacific sacoglossans have functional chloroplast retention or kleptoplasty? Most northeastern Pacific species retain chloroplasts for varying lengths of time, but only three species have functional retention (*Alderia modesta*, *Elysia hedgpethi*, and *Elysia diomedea*) and it is short-term for the first two (Table 5). The phenomenon of kleptoplasty has been well reviewed (Clark et al., 1990; Clark, 1992; Williams & Walker, 1999). Yet, details for the majority of Pacific species are lacking or are extrapolated from other geographic regions. Based on the information available, most northeastern Pacific species are strictly heterotrophic, and thus their herbivory may be more important in damaging their host plants than species with multiple modes of nutrition.

Aspects of feeding behavior that have been well studied in one species, *Placida dendritica*, are the patterns and ecological consequences of gregarious feeding (Long, 1969; Clark, 1975; Trowbridge, 1991b). On the algal host *Codium setchellii*, 97.4% of the slugs are group members on Oregon shores; on *C. fragile*, 60.3% of slugs are group members; on *Bryopsis*, slugs do not generally aggregate (Trowbridge, 1991b). Gregarious feeding and intraspecific feeding facilitation documented for *P. dendritica*, are unusual in sacoglossans and even in marine herbivores (Trowbridge, 1991b).

Sacoglossan herbivory may substantially reduce algal host populations when slug densities and/or per capita feeding rates are high. For northeastern Pacific species, grazing by *Placida dendritica* and *Stiliger fuscovittatus* may be ecologically important to *Codium* and *Polysiphonia* populations, respectively (Case, 1972; Trowbridge, 1992a, 1993b, 1998b). Case (1972:59) remarked that a "large population of *S. fuscovittatus* apparently can reduce the volume of

Polysiphonia to such a degree that food becomes a limiting factor."

The role of epiphytes in determining patterns of sacoglossan attack of host plants has not been well explored. Wahl & Hay (1995) reported that epiphytes could either enhance herbivore attack ("shared doom") or decrease it ("associational resistance"). For *Placida dendritica*, algal hosts of *Codium fragile* with the epiphyte *Ceramium codicola* (specific to *Codium*) were more attractive than hosts free of epiphytes (Trowbridge, 1993b). This may be due to several different processes: (1) epiphytes provide slugs a refuge from predators, (2) epiphytes ameliorate physical conditions (e.g., desiccation stress during emergence and wave force during submergence), (3) slugs attack hosts whose defenses are compromised by epiphytes, and (4) red algal epiphytes may induce larval settlement and metamorphosis (Trowbridge, 1993b). Of the northeastern Pacific sacoglossan species, only two are known to consume epiphytes, namely *Heruaea vaucouvereensis* that feeds selectively on the epiphytic diatom *Isthmia nervosa* that coats intertidal macrophytes in summer and fall, and *Stiliger fuscovittatus* that eats epiphytic (and non-epiphytic) species of *Polysiphonia*. Given the important ecological roles epiphytes may have in mediating slug-host associations, the ecological function should be explored more fully for different sacoglossans.

In terms of sacoglossan energetics, there has been little comprehensive work for any northeastern Pacific species, although there are data for different aspects for different species. The general equation for the energy budget of an organism is:

$$\begin{aligned} \text{Consumption} &= \text{Production} + \text{Fecundity} \\ &+ \text{Respiration} + \text{Excretion} \\ &+ \text{Secretion.} \end{aligned}$$

There have been several studies that have provided estimates of feeding rates for *Olea*, *Alderia*, *Placida*, and *Aplysiopsis* (Crane, 1971; Trowbridge, 1991a, b, 1992a, 1993a, b). There have been a few calculations from per capita feeding rates to population estimates of slug herbivory (Trowbridge, 1992a, 1993a, b). Activity levels and respiration have not been explored for northeastern Pacific species (but see work by Clark, 1975 on Atlantic *Placida dendritica* and *Ercolania fuscata*); fecundity values (section below) are scarce. Thus, there is insufficient information even for the most abundant sacoglossans to determine energetics. Because sacoglossans are suctorial stenophagous feeders, extrapolations from generalist consumers would provide unrealistic estimates.

REPRODUCTION, DEVELOPMENT AND GROWTH

Reproduction

Mating and spawning have been documented for several northeastern Pacific species (Gonor, 1961; Seelemann, 1967;

Baba & Hamatani, 1970; Crane, 1971; Case, 1972; Ferreira & Bertsch, 1975; Millen, 1980; Trowbridge, 1992b, 1993d). The minimum size of mating individuals is surprisingly small. For example, *Olea hansineensis* forms courtship groups when 2 mm long, and reproduction commences at 4 mm (Crane, 1971; Chia & Skeel, 1973). In *Stiliger fuscovittatus*, the minimum size of egg mass production is 3 mm (Case, 1972). Mating generally involves paired copulatory behavior typical of most opisthobranchs. *Alderia modesta*, however, inseminates conspecifics hypodermically (Hand & Steinberg, 1955), as do *Ercolania boodleae* (Baba & Hamatani, 1970) and *E. fuscata* (Gascoigne, 1978). Fertile eggs are produced at least 10 days after copulation for *Stiliger fuscovittatus* (Case, 1972), although the generality for other species is not known. Like other opisthobranchs, sacoglossans store sperm obtained from mating partners; the longevity of these allosperm is not known. Opisthobranch allosperm and ova are mixed during egg mass deposition (reviewed by Hadfield & Switzer-Dunlap, 1984) but specific information for sacoglossans is lacking.

Chia & Skeel (1973) and Seelemann (1967) have reported high fecundity values for *Olea hansineensis* and *Alderia modesta*, respectively. For example, *A. modesta* produces about 1000 eggs per day on European shores. On Californian shores, young adults of *A. modesta* lay approx. one egg mass per day over a 2 to 3 week period in the laboratory; furthermore, there was no difference in the frequency of clutch production for planktotrophic vs. lecithotrophic clutches (P. Krug, personal communication 2000). Case (1972) reported much lower values for *Stiliger fuscovittatus*: about 212–232 eggs per day. Egg masses have been described for several species (Gonor, 1961; Lance, 1962; Hurst, 1967; Greene, 1968; Chia, 1971; Case, 1972).

Deposition of the masses (oviposition) is usually on the host plants or other macroalgae in the habitat (e.g., Gonor, 1961; Lance, 1962; Greene, 1968; Case, 1972). In contrast to juveniles and adults, the egg masses, embryos, and larvae do not contain chloroplasts (Greene, 1968; Trench et al., 1969; Case, 1972; Trowbridge, personal observations); thus, retained chloroplasts are newly acquired by each generation. Over 80% of egg masses laid by *Stiliger fuscovittatus* were produced between 11 pm and 8 am (Case, 1972). The generality of nocturnal deposition is not known.

With the exception of lecithotrophic *Alderia modesta* (Krug, 1998b), all species have small ova with mean diameters between 55 and 95 μm (Table 6). In most cases there is one ovum per capsule; the four exceptions are *Lobiger souverbii*, *Elysia diomedea*, *E. hedgpethi*, and *Stiliger fuscovittatus* (Table 6). Case (1972) reported that none of the embryos with two ova per capsule developed for *S. fuscovittatus*. Three other embryonic details are particularly noteworthy. (1) Embryonic development was 10% faster when egg masses were attached to algal hosts

than when attached to glass or floating freely in seawater (Case, 1972). (2) Embryonic synchrony occurs within individual egg masses of *S. fuscovittatus* (Case, 1972). (3) Hatching rates vary between 95% and 99% for *S. fuscovittatus* (Case, 1972). The generality of these patterns merits further investigation for other northeastern Pacific sacoglossans.

Of the northeastern Pacific species for which data are available, all but one have planktotrophic larvae (Table 6); *Alderia modesta* is poecilogonous and produces both planktotrophic and lecithotrophic larvae (Krug, 1998a, b, 2001; Krug & Zimmer, 2000a). Veligers and shells have been described by Hurst (1967), Greene (1968), Case (1972), Goddard (1984), and Krug (1998a, b). The larval types of the majority of warm-temperate to tropical species have not yet been described. Overall, information on development is available for only half of the known northeastern Pacific species (Table 6).

Larval Development and Metamorphosis

Strathmann (1987) reviewed larval attributes of northeastern Pacific sacoglossans. None of the species has been raised through its life cycle with the exception of *Alderia modesta* from southern California (Krug, 1998a, 2001; Krug & Manzi, 1999; Krug & Zimmer, 2000a, b) and from Europe (Seelemann, 1967) and *Aplysiopsis enteromorphae* (P. Krug, personal communication, 2000). In fact, only a few sacoglossan species with planktotrophic larvae have been successfully raised through their lengthy larval growth period to larval competency, settlement, and metamorphosis (e.g., Krug & Zimmer, 2000); numerous other attempts have failed (e.g., Case, 1972; Trowbridge, unpublished data). This area of research requires more attention, particularly in terms of the rates of larval growth and the nature and specificity of cues inducing larval settlement and metamorphosis. Larvae of *A. modesta* responded to water-soluble algal cues as well as surface-associated compounds (Krug & Manzi, 1999; Krug & Zimmer, 2000a; Krug, 2001). The little quantitative experimental data on sacoglossans (Trowbridge & Todd, 2001) indicate that the paradigm of metamorphosis only in response to adult prey is a significantly over-simplified view based in large part on insufficient controls to test alternative hypotheses (see Havenhand, 1991; Trowbridge & Todd, 2001).

The spatial and temporal patterns of sacoglossan recruitment have not been extensively examined, particularly at the regional scale. On a local scale (e.g., at a given site), *Placida dendritica* recruited more abundantly to algal hosts transplanted to (1) wave-sheltered coves than on closely adjacent points (Trowbridge, 1992a), (2) desiccation-prone microhabitats than to low-stress ones (Trowbridge, 1998b), and (3) horizontal substratum than to closely adjacent vertical substratum (Trowbridge, unpublished data). Peak recruitment rates are 200–400 slugs

Table 6
Developmental features of northeastern Pacific sacoglossans

Species	Ovum diameter (μm)	Ova per capsule	Shell length at hatching (μm)	Veliger type	References
<i>Lobiger souverbii</i>	(54.6–66.5)*	Up to 5	no data	type I	Clark & Goetzfried (1978), Clark & Jensen (1981)
<i>Elysia hedgpethi</i>	70	1–2	99, 109 105 \pm 20.6	type I	Greene (1968), Strathmann (1987), J. Goddard (personal communication, 2000)
<i>Elysia diomedea</i>	no data	6–14	no data	no data	Bertsch & Smith (1973)
<i>Aplysiopsis enteromorphae</i>	66–70	1	107–113 109 \pm 1.7	type I	Gonor (1961), Greene (1968), Goddard (1984), Strathmann (1987)
<i>Aplysiopsis oliviae</i>	no data	1	no data	no data	Millen (1980)
<i>Hermaea vancouverensis</i>	no data	1	no data	type I	Trowbridge (unpublished data)
<i>Alderia modesta</i>	68–80 (70–82)*	1	90–124	type I	Hand & Steinberg (1955), Hurst (1967), Thompson (1976), Clark & Goetzfried (1978), Strathmann (1987), Krug (1998b)
	105	1	186 (190)*	type II	Seelemann (1967), Krug (1998b)
<i>Ercolania boodlea</i>	?	1	?	?	Baba & Hamatani (1952)
<i>Olea hansineensis</i>	81–120 (capsule)	1	110.7	type I	Agersborg (1923), Hurst (1967), Strathmann (1987)
<i>Placida dendritica</i>	no data (47–77+)* (72.0 \pm 5.1)*	1	82–112 (113–127)* 97 \pm 15.0	type I	Greene (1968), Kress (1971), Clark (1975), Thompson (1976), Strathmann (1987)
<i>Stiliger fuscovittatus</i>	70–95 (66.5)*	1(–2)	110–150	type I	Lance (1962), Case (1972), Clark & Goetzfried (1978), Strathmann (1987)
<i>Ercolania fuscata</i>	(60, 66.5) (64.5 \pm 2.0)*	no data	no data	type I	Clark (1975), Clark & Goetzfried (1978), Clark & Jensen (1981)

(*) Indicates from regions other than NE Pacific shores.

algal thallus⁻¹ month⁻¹ (Trowbridge, 1992a). Given that most northeastern Pacific species appear to have planktotrophic larvae (Table 6), information about the role of nutrient concentrations, phytoplankton concentrations, and upwelling patterns that affect larval survival, growth, and settlement clearly merits attention (e.g., Trowbridge, 1992b). Many sites appear to have high densities of sacoglossan larvae, not because the benthic algal hosts are more attractive or abundant (Trowbridge, unpublished data) but because of the influence of oceanographic conditions on these factors. For example, Seal Rock and Strawberry Hill, Oregon, consistently have high densities of many species of sacoglossans (as well as other opisthobranchs) every spring and summer (in contrast to what was initially reported by Sphon, 1972); these two sites are recruitment "hot-spots" for many types of larvae including barnacles, mussels, and sacoglossans (Menge, 1992; Menge et al. 1997; Trowbridge, 1992b; B. Menge, personal communication 1996). Such meso-scale ocean-

ographic conditions may account for some of the apparent patchiness of sacoglossan populations.

Post-Metamorphic Growth

Another enigmatic period in sacoglossan life cycles is the post-metamorphic juvenile stage, particularly the behavior, feeding habitats, and growth rates of juveniles. For *Alderia modesta* on European shores, juveniles (0.8 mm long) feed, rapidly develop cerata, and produce eggs when 10 days old at a length of 3 mm (Seelemann, 1967). On the shores of southern New England, the life span of *A. modesta* was estimated as 2–6 months (Clark, 1975); information for northeastern Pacific populations is not available. Information on growth of *Olea hansineensis* also indicates a rapid life cycle, with 5 days to reach 1 mm and 2–3 weeks to reach sexual maturity (Crane, 1971; Chia & Skeel, 1973). Clark (1975) and Jensen (1983) recorded the growth of Atlantic populations of *Ercolania fuscata* on multiple algal diets (*Cladophora*,

Chaetomorpha, *Cladophoropsis*). Furthermore, Clark (1975) conducted reciprocal feeding experiments to determine the importance of algal source of slugs vs. intrinsic food quality; he also documented that slugs were, on average, larger on *Chaetomorpha* on the shore but more abundant on *Cladophora*. Jensen (1983) also recorded the growth of *Lobiger souverbii* on *Caulerpa racemosa* (on Atlantic shores).

Fretter (1941) described the gut of sacoglossans and suggested that species could ingest large quantities in short periods, given the structure of the gut. If high ingestion corresponds to rapid growth, then sacoglossans have the potential for extremely rapid growth. Based on short-term growth rates of *Placida dendritica*, slugs increase in mass at about 25% body mass per day in the laboratory on *Codium* spp. and at 30–40% on *Bryopsis corticulans* (Trowbridge, 1991a). Growth rates in the field were calculated by outplanting algal hosts (with no slugs) and measuring the body size of recruits after different intervals of time (Trowbridge, 1992a). Based on these data, Trowbridge (1991a) estimated the longevity of *P. dendritica* to be 1–2 months. Case (1972) observed that post-settlement juveniles of *Stiliger fuscovittatus* preferred new growth (i.e., terminal young branches) of *Polysiphonia brodiaei* to older, highly corticated algae, and he also suggested that juveniles could starve in the presence of host plants, presumably if young branches were not available. *S. fuscovittatus* reached sexual maturity in less than 2 months after metamorphosis; slugs reproduced for several months, then died (Case, 1972).

POPULATION DYNAMICS AND STRUCTURE

Seasonality

Phenological information for northeastern Pacific sacoglossans is rather meager. For all the northeastern Pacific species, the inferred seasonalities (Figure 2) are based on published collection records, my own collection records (C. Trowbridge, unpublished data), or personal communications (J. Goddard, 2000; S. V. Millen, 2000). More sampling and observations are needed before reliable phenological data are available for the less well-studied 19–20 sacoglossan species. Collection records for species in the Gulf of California and southward may indicate that sacoglossans are present much of the year; quantitative abundance data would assist in the interpretation of presence/absence data.

The most comprehensive and quantitative data are on *Placida dendritica* on Oregon shores (Trowbridge, 1992b) where the species occurred on intertidal algal hosts from April to September with occasional slugs being found in March and October (Figure 2). *Aplysiopsis enteromorphae* also appears to be primarily a spring and summer species on Oregon shores (Goddard, 1984:146, J. Goddard, personal communication, 2000; Trowbridge, 1993a, d). Monthly observations over the course of 1 year

(September 1975 to September 1976) at Scott Creek, Santa Cruz County, California showed that *A. enteromorphae* was present year around in high intertidal, outer coast pools; the species peaked in abundance in September and October and declined sharply in November (J. Goddard, unpublished observations). Egg masses were produced year around but were most abundant in September and October (J. Goddard, unpublished observations). The spring and summer seasonality inferred for *Elysia hedgpethi* (Figure 2) is based on my observations for Seal Rock and Boiler Bay, Lincoln County, Oregon (C. Trowbridge, unpublished data). *Elysia hedgpethi* and its eggs were found on *Codium fragile* in La Jolla, California in January and February 2000 (J. Goddard, unpublished observations). Finally, *Stiliger fuscovittatus* in San Francisco Bay, California was most abundant in fall and early winter (Case, 1972); whether the species exhibits a similar phenology on open-coast shores is not yet known.

Several authors (Miller, 1962; Clark, 1975) have categorized opisthobranchs based on whether they are (1) annual to subannual with multiple generations per year or (2) perennial. Based on seasonality data (Figure 3), this dichotomy is difficult to apply to northeastern Pacific species. *Placida dendritica*, *Alderia modesta*, and *Stiliger fuscovittatus* could be assigned to the first category as they have continual recruitment, rapid growth, and early reproductive maturity (Case, 1972; Trowbridge, 1992a, b, 1993c, d). *Aplysiopsis enteromorphae* is clearly subannual in Oregon with a single generation per year (Trowbridge, 1993a, d). For other species, there is not sufficient information to categorize them. Some authors have suggested that spring to summer seasonal patterns reflect slugs tracking seasonally available algal species. Yet, for *P. dendritica*, *Elysia hedgpethi*, *A. enteromorphae*, *A. modesta*, and *S. fuscovittatus*, the algal hosts are present all year, and thus, the seasonal disappearance is due to constraints other than food limitations. For *Hermaea vancouverensis*, the diatom *Istlmia nervosa* is seasonally abundant with peak densities from July to September on Oregon open-coast shores (Trowbridge, personal observations) and perhaps earlier in California; spatio-temporal variation in diatom abundance throughout the slug's range merits examination. Phenological information for three of the northeastern Pacific species, also found on Atlantic shores, is summarized by Clark (1975) and Bleakney (1996); comparable data for Pacific shores are lacking.

Sacoglossan Abundance

For most northeastern Pacific sacoglossan species, population density information is qualitative: abundant, common, frequent, rare, etc. (e.g., Lance, 1961; Steinberg, 1963; Sphon & Lance, 1968; Roller & Long, 1969; Roller, 1970b; Williams & Gosliner, 1971; Gosliner & Williams, 1973). Quantitative data are slowly being collected. For pool-dwelling species such as *Aplysiopsis enter-*

Species		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Placida dendritica</i>	N			■	■	■	■	■	■	■	■		
	S				■	■	■	■	■	■			
	G						■						■
<i>Elysia hedgpethi</i>	N			■	■	■	■	■	■	■	■		
	S	■	■		■	■	■	■	■	■			
	G		■	■	■	■	■	■	■	■			■
<i>Aplysiopsis enteromorphae</i>	N			■	■	■	■	■	■	■	■		
	S			■	■	■	■	■	■	■	■		
	G												■
<i>Alderia modesta</i>	N	■	■	■	■	■	■	■	■	■	■	■	■
	S	■	■	■	■	■	■	■	■	■	■	■	■
	G												
<i>Stiliger fuscovittatus</i>	N			■	■	■	■	■	■	■	■		
	S	■	■	■	■	■	■	■	■	■	■	■	■
	G												
<i>Olea hansineensis</i>	N						■	■	■	■			
	S												
<i>Hermaea vancouverensis</i>	N			■	■	■	■	■	■	■	■		
	S			■	■	■	■	■	■	■	■		
<i>Aplysiopsis Oliviae</i>	N										■	■	■
	S												
<i>Elysia diomedea</i>	G									■			■
<i>Oxynoe panamensis</i>	G												
<i>Berthelina chloris</i>	G												
<i>Lobiger souverbii</i>	G												
<i>Polybranchia viridis</i>	G												
<i>Cyerce orteai</i>	G												
<i>Ercolania fuscata</i>	G												

Figure 2. Seasonality of northeastern Pacific sacoglossan species in three major regions: N (north) indicates Alaska to Oregon, S (south) indicates California, and G (gulf) indicates the Pacific coast of Baja California, the Gulf of California, and southward to the equator. Shaded cells represent slug presence and ? represents presumed occurrence but no published reports, personal observations, or personal communications. Data from Bergh, 1894; Cockerell & Eliot, 1905; MacFarland, 1924, 1966; Sowell, 1949; Hand & Steinberg, 1955; Gonor, 1961; Keen & Smith, 1961; Lance, 1961, 1962, 1966, 1996; Marcus, 1961; Smith, 1961; Hurst, 1967; Farmer, 1967; Marcus & Marcus, 1967; Dushane & Sphon, 1968; Lewin, 1970; Sphon & Mulliner, 1972; Bertsch, 1971, 1973; Robilliard, 1971; Sphon, 1971; Bertsch & Smith, 1973; Chia & Skeel, 1973; Gosliner & Williams, 1973; Williams & Gosliner, 1973; Larson & Bertsch, 1974; Ferreira & Bertsch, 1975; Lambert, 1976; Behrens & Tuel, 1977; McLean, 1978; Millen, 1980, 1989; Goddard, 1984, 1987, personal communication, 2000; Jaeckle, 1984; Foster, 1987; Trowbridge, 1993a, d, 1994, unpublished data; Goddard et al., 1997; Bertsch et al., 1998; Lance, 1998.

omorphae, Trowbridge (1993a) reported values of up to 50% of pools at individual sites on Oregon shores. For mat-dwelling species such as *Alderia modesta*, population estimates range from tens to thousands per m² (Trowbridge,

1993c, d). Lewin (1970) reported that *Oxynoe panamensis* was abundant at about one slug per m². For sacoglossan species inhabiting separate, upright branching algal hosts, estimates of abundance range up to 70% of hosts for *Pla-*

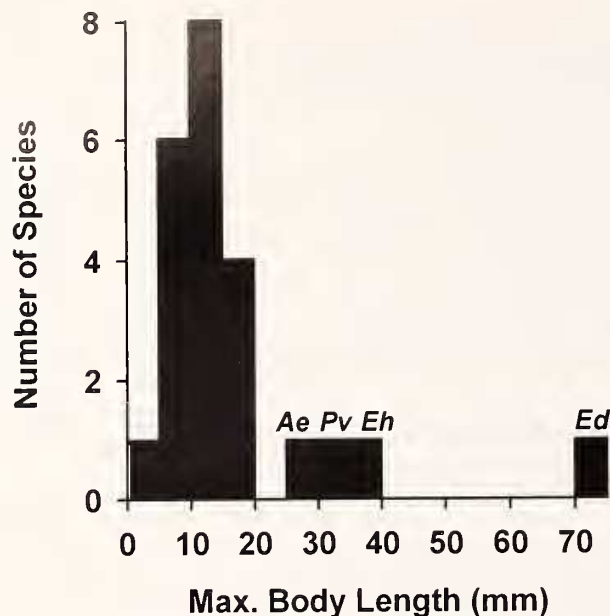


Figure 3. Maximum size–frequency distribution of northeastern Pacific sacoglossans. Abbreviations for the larger species are as follows: Ae = *Aplysiopsis enteromorphae*, Pv = *Polybranchia viridis*, Eh = *Elysia hedgpethi*, Ed = *Elysia diomedea*. Data based on Agersborg, 1923; MacFarland, 1966; Marcus & Marcus, 1967, 1970b; Baba & Hamatani, 1970; Keen, 1971; Chia & Skeel, 1973; Beeman & Williams, 1980; Goddard, 1984; Behrens, 1991a; Trowbridge, 1993a, c; Bertsch et al., 1998; Valdés & Camacho-García, 2000.

Placida dendritica (Trowbridge, 1993b). Case (1972) reported abundance values of *Stiliger fuscovittatus* in a range of ways: total number of animals found, number of slugs per ml of algal host, and number of slugs per m² of substrata. Other authors such as Clark & DeFreese (1987) have reported abundance values as number of slugs per gram dry mass of algae. Dry mass values, however, are not logistically possible for all sites (e.g., marine reserves) or for all algal hosts (e.g., *Vaucheria* spp., which forms mats binding algae and sediments together, the diatom *Isthmia nervosa*, which forms colonies attached to intertidal macrophytes, or *Codium setchellii*, which is relatively scarce (Trowbridge, 1996)). For none of the northeastern Pacific species is there sufficient population data to test whether the positive association between latitude and peak slug density (reported by Clark & DeFreese, 1987 for Atlantic species) also occurs in our region. Given that past collection locations are known for most species (Tables 2, 3), such regional abundance information should be feasible to document.

Population Structure

Detailed investigations of population structure have been reported for four species: *Stiliger fuscovittatus* (Case, 1972), *Alderia modesta* (Trowbridge, 1993d),

Aplysiopsis enteromorphae (Trowbridge, 1993a, d), and *Placida dendritica* (Trowbridge, 1992b). Detailed length–frequency data (e.g., 871 individuals of *Stiliger fuscovittatus*: Case, 1972) can provide valuable insight into the timing of juvenile recruitment, the rate of juvenile and adult growth, and the timing of adult mortality. When supplemented with environmental data (see Trowbridge, 1992b), population structure data can be a powerful tool for investigating sacoglossan ecology. Because many ecological processes (e.g., fecundity, predation, etc.) are size-dependent, maximum body size of a given species (Figure 3) is valuable and should be included in future collections.

ABIOTIC FACTORS

The importance of physical or abiotic factors in structuring sacoglossan populations has been generally assumed but rarely demonstrated. Notable exceptions include descriptive and experimental work by Case (1972) and Trowbridge (1992a, b). The salinity tolerance of *Stiliger fuscovittatus* and *Alderia modesta* presumably affects the spatio-temporal patterns of slug populations within estuaries. Case (1972) reported that 50% of *S. fuscovittatus* individuals tested died within 18 hr when held in 10 ppt water and 50% died within 72 hr at 13 ppt; slugs survived well at salinities of 21 and 33 ppt. Given that salinities in San Francisco Bay dropped to 4 ppt for over 24 hr, Case's suggestion that low salinity caused the dramatic observed decline in slug population density seems well supported. Comparable details have been described for the marsh slug *A. modesta* on European shores (Seelemann, 1968). There was geographic variation in salinity tolerance by *A. modesta*; both high and low salinities disrupted embryonic development and egg production (Seelemann, 1968). Presumably, these autecological responses will dictate species' distributions within bays. Behrens (1980), summarizing the literature for San Francisco Bay, reported that four species occurred in the bay: *A. modesta*, *S. fuscovittatus*, *Elysia hedgpethi*, and *Placida dendritica*. The salinity tolerance of the latter two species is not known, nor is it known for *Aplysiopsis enteromorphae* in high intertidal pools or on estuarine mudflats (Trowbridge, 1993a, d).

The role of fluctuations in air and seawater temperature also merits consideration. Case (1972) reported that adult *Stiliger fuscovittatus* was eurythermal. Both low temperature (4°C) and high (19–23°C) had little effect on adult slugs, despite the narrow temperature range slugs encountered in the bay (11–16°C) (Case, 1972). Furthermore, Trowbridge (1992b) noted that the maximum size of *Placida dendritica* increased significantly with increased seawater temperature. With the availability of temperature chart recorders that could be attached to rocky surfaces on the shores, our understanding of the

contribution of atypically hot or cold days to population fluctuations of slugs should improve.

Finally, the influence of wave exposure on sacoglossan population structure and dynamics has long been surmised. The little information available is mostly indirect. Case (1972) monitored the population abundance of *Stiliger fuscovittatus* along a sea wall with a strong wave exposure gradient; slugs were most abundant at site 2 (site 1 was most sheltered, site 8 was most exposed). He surmised that *S. fuscovittatus* could not persist on the open coast but suggested this hypothesis should be tested experimentally. Other authors, including myself, have subsequently found the species on the open coast, although albeit in comparatively wave-protected habitats (e.g., Seal Rock, Oregon where a series of rocks breaks the wave force considerably). Current techniques now available to measure wave force and water flow in a quantitative fashion could be usefully applied to opisthobranch studies.

BIOTIC INTERACTIONS

Predation

Opisthobranchs have a repertoire of defenses against potential predators (e.g., reviews by Thompson, 1976; Di Marzo et al., 1993; Cimino & Ghiselin, 1998; Cimino et al., 1999). For northeastern Pacific sacoglossan species, the support for chemical and/or behavioral defenses is relatively meager (Table 7). Trowbridge (1994) tested the pH of four species of sacoglossans; while they all reduced their surface pH when physically disturbed, only one was acidic (*Aplysiopsis enteromorphae*). Three of the four species were readily consumed by a suite of ecologically relevant predators in spite of any purported defenses such as cerata waving and/or autotomy. However, one of these, *Stiliger fuscovittatus*, was not consumed by the carnivorous *Roboastra tigris* (Lance, 1997). *Aplysiopsis enteromorphae* was also not consumed by a variety of predators, but the basis of the slugs' unpalatability has not been explored (Trowbridge, 1994).

In a 12-day field experiment conducted in Oregon, *Alderia modesta* abundance was significantly reduced on exposed algal mats and in cage controls compared to in full predator-exclusion cages (Trowbridge, 1994). These results indicate that intense predation did significantly reduce slug populations; moreover, observational evidence from Váder (1981) and experimental evidence from Trowbridge (1993c, 1994) indicates that bird, fish, and crab predation can be important in reducing slug densities. Bleakney (1996) suggested that the "potent, sickly-sweet perfume exuded" by *A. modesta* may be an effective defense against spiders, beetles, and bugs; this intriguing hypothesis merits experimental testing. Predator exclusion experiments need to be conducted for other sacoglossan species, particularly for the warm-temperate to

tropical species that may experience more intense predation than their high-latitude counterparts.

The tropical to subtropical sacoglossan *Elysia diomedea* contains secondary metabolites named tridachione (after the slug's previous genus name *Tridachiella*) and 9, 10-deoxytridachione; it is unclear whether these compounds are derived directly from dietary sources, from retained functional chloroplasts, or synthesized *de novo* (Ireland et al. 1978; Ireland & Faulkner 1981). Vardaro et al. (1992) reported that *Placida dendritica* on Mediterranean shores produced polypropionate compounds *de novo* and that they were not localized in specific tissues. Furthermore, Di Marzo et al. (1993) reported that the Mediterranean *P. dendritica* was unpalatable to fishes; in contrast, Trowbridge (1994) reported that fishes readily consumed specimens on Oregon shores. The source of this variation is intriguing; whether it is due to cryptic species (morphologically similar species that are often confused as a single species), geographic variation in capacity to synthesize compounds *de novo*, or to other factors is not known. The source of the secondary metabolites, however, is seemingly not the algal diet (Cimino et al., 1999).

Information on the predation of sacoglossan larvae and egg masses is meager. Caprellid amphipods may prey upon swimming veliger larvae or setting juveniles (Kæstner, 1967, cited by Case, 1972). There are some details of egg predation by the sacoglossan *Olea hansineensis*. Crane (1971:58) wrote that "adults were observed to recoil violently from their own egg mass. . . . Apparently, contact is necessary for recognition of their egg masses." This aversion response is not only to their egg masses but also to those of conspecifics (S. V. Millen, personal communication, 2000).

In all of the cases above, the slugs are consumed directly by predators. Predation, however, can have indirect effects on slugs (Case, 1972) when consumers (e.g., birds) consume the substrata (e.g., mussels) upon which the slugs' algal food grows. Indirect effects of predators or generalist herbivores would be most important in cases in which the slugs' algal hosts are epibionts, growing on top of a shellfish or an alga. The importance of this mechanism in regulating slug populations has not yet been explored.

Competition

In terrestrial systems, there is extensive theoretical and empirical information on the role of interspecific and intraspecific competition among stenophagous herbivores such as phytophagous insects. In marine systems, the topic has barely been addressed. In many cases, sacoglossans occur on host plants not used by other grazers (Trowbridge, 1992a). In other cases, such as *Aplysiopsis enteromorphae*, the slugs coexist with prosobranch gastropods and small crustaceans (e.g., amphipods, isopods) (Trow-

Table 7
 Potential defensive adaptations of northeastern Pacific sacoglossans and the animals' palatability to predators

Sacoglossan species	Potential defenses	Palatability	References
<i>Oxynoe patanaensis</i>	algal metabolite sequestration (caulterpin & caulpericin), toxic secretion, tail autotomy	toxic secretion lethal to fish	Doty & Aguilar-Santos (1970), Lewin (1970)
<i>Lobiger souverbii</i>	discharge white substance; lobe autotomy	toxic secretion lethal to fish	Kay (1964), Gosliner (1987), Gosliner et al. (1996)
<i>Elysia hedgpethii</i>	no data	not consumed by fishes, crabs, or <i>Roboastra tigris</i>	Trowbridge (1994), Lance (1997)
<i>Elysia diomedea</i>	tridachione & 9, 10-deoxytridachione (secondary metabolite)	no data?	Ireland et al. (1978), Ireland & Faulkner (1981)
<i>Aphysiopsis enternormorphae</i>	wave & shed cerata; reduce body pH from neutral to pH = 4	unpalatable to fishes and crabs; source not known	Trowbridge (1994)
<i>Alderia modesta</i>	reduce body pH but still basic; peculiar, sickly sweet smell	palatable to fishes & crabs	Hand & Steinberg (1955), Trowbridge (1994), Bleakney (1996)
<i>Ercolania boodlea</i>	exude milky-white fluid	no data?	Baba & Hamatani (1970)
<i>Placida dendritica</i>	wave & shed cerata; reduce body pH when disturbed from basic to neutral; Mediterranean animals synthesize polypropionates <i>de novo</i> (e.g., placidene-A)	Oregon animals palatable to fishes & crabs; Mediterranean animals unpalatable to fishes	Vardaro et al. (1992), Di Marzo et al. (1993), Trowbridge (1994), Cimino et al. (1999)
<i>Stiliger fuscovittatus</i>	wave & shed cerata; reduce body pH when disturbed from basic to neutral	palatable to fishes & crabs; not consumed by <i>Roboastra tigris</i>	Trowbridge (1994), Lance (1997)

bridge, 1993a). On northeastern Pacific shores, *Placida dendritica* and *Elysia hedgpethi* coexist on the same host species and even occasionally on the same thalli (D. Behrens, personal communication, 2000; C. Trowbridge, personal observations); whether the two species facilitate one another, inhibit one another, or have no effect deserves future consideration.

Finally, for the two species that often occur at very high densities, *P. dendritica* and *Alderia modesta*, intraspecific interactions merit investigation. Trowbridge (1991b) demonstrated that small individuals of *P. dendritica* inhibit the feeding and growth of large conspecifics (i.e., intraspecific competition); in contrast, large slugs facilitate the feeding and growth of small and large conspecifics (facilitation). For *A. modesta*, population density and body size are inversely related on a regional scale (Trowbridge, 1993c, d). Whether this pattern reflected intraspecific competition or other mechanisms (e.g., high recruitment coupled with high mortality) has not been investigated.

SPECIES IDENTITY AND VARIATION

The majority of sacoglossans are described based on morphology, especially radular tooth shape and size and various attributes of the reproductive system. In few cases has the biological species concept been tested by controlled matings of seemingly conspecific animals. Thus, it is frequently difficult to determine whether observed variation is best considered inter-specific or intra-specific. Molecular techniques offer independent methods to test the validity of morphospecies. To date, extremely few molecular studies of this sort have been conducted on sacoglossans (or other opisthobranchs). Theisen & Jensen (1991) investigated genetic variation of European species (including the species *Alderia modesta*) with allozymes. Krug (1998a, b) and Trowbridge (unpublished data) investigated variation in the mtDNA gene cytochrome oxidase subunit I (COI) of *A. modesta*, *Placida dendritica*, and *Ercolania boodlea*. Thollesson (1999) and Trowbridge (work in progress) have sequenced portions of the mtDNA gene 16S rRNA in *P. dendritica*. I predict that molecular techniques will result in the splitting of cosmopolitan species (e.g., *Placida dendritica*) into sibling species, analogous to work on other taxa (e.g., Knowlton, 1993; Geller et al., 1997). *P. dendritica* has been a controversial species for decades (Thompson, 1973, 1976, 1988; Gosliner, 1987; Bleakney, 1989, 1990; Trowbridge, 1997; Burn, 1998; references therein) due to morphological, physiological, and ecological variation. Molecular details may soon resolve whether *P. dendritica* is the appropriate name for the northeastern Pacific species: the species was described from specimens collected from Torbay, England.

Molecular techniques may resolve many of the problematic taxonomic issues as well as assist with the as-

signment of new undescribed species to correct genera. The placement of many species in the families Hermaeiidae and Limapontiidae (*sensu* Jensen, 1996) has been very problematic, rendering the sacoglossan literature difficult to follow. For example, the species *Aplysiopsis enteromorphae* has been placed in three different genera since 1905; many other species have been transferred between genera (in different families) as our understanding has improved. Molecular research may assist in resolving future taxonomic difficulties (e.g., with the undescribed species shown in Table 1). Finally, molecular information could contribute substantially to the questions of larval dispersal, gene flow host specificity, and other ecological or evolutionary issues.

PROSPECTUS

The field of sacoglossan biology is wide open with extensive areas of unexplored issues. Some of the priority areas for future research on northeastern Pacific sacoglossans are:

1. Investigate the northeastern Pacific sacoglossan fauna from the Gulf of California south to the equator. The investigation of this tropical to subtropical region will undoubtedly raise our estimate of sacoglossan species richness.
2. Document the population structure and dynamics of species, including the seasonality of slug and spawn occurrence, adult immigration, and frequency of adults over-wintering. If sacoglossans are indeed particularly susceptible to environmental degradation, habitat loss, and anthropogenic change (Clark, 1994), basic population information about these species is essential to provide a baseline from which to evaluate future change.
3. Document the host-plant associations in more comprehensive detail, both spatially and temporally. Even specialized associations change on ecological and evolutionary time scales. Thus, understanding the conditions under which trophic flexibility does occur is biologically significant.
4. Study the feeding and foraging behavior, particularly the existence of any temporal patterns (tidal or diurnal/nocturnal). Ecological theories about feeding specificity are frequently based on assumptions of vulnerability of slugs to potential predators; basic information about when and where sacoglossans feed is crucial to evaluating their risk to visual predators.
5. Investigate the relative importance of kleptoplastic vs. heterotrophic sources of nutrition. The new technique of PAM fluorometry provides us with the means of rapidly and non-invasively screening slugs for photosynthetic activity (S. Williams, 2000; personal communication, 2000).
6. Quantify patterns of larval growth, metamorphosis, post-larval growth, and fecundity.

7. Document the effect of physical variables such as salinity, temperature, irradiance, turbidity, etc., as well as UV light, pesticides, and other types of coastal pollution on slug population dynamics (see Clark, 1975, 1994, 1995).
8. Investigate the patterns of genetic variation within and among species; such molecular techniques will aid the correct placement of the taxonomically challenging, undescribed sacoglossans on northeastern Pacific shores as well as contribute to the understanding of sacoglossan population structure and dispersal.

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LITERATURE CITED

- AGERSBORG, H. P. K. 1923. Notes on a new cladohepatic nudibranch from Friday Harbor, Washington. *The Nautilus* 36: 133–138.
- BABA, K. 1938. Opisthobranchia of Kii, Middle Japan. *Journal of the Department of Agriculture, Kyūshū Imperial University* 6:1–19.
- BABA, K. 1949. Opisthobranchia of Sagami Bay Collected By His Majesty the Emperor of Japan. Iwanami Shoten: Tokyo. 194 pp.
- BABA, K. 1974. Some comments on *Lobiger souverbii* Fischer, 1856, re-identified, of Japan (Opisthobranchia: Sacoglossa: Lobigeridae). *The Veliger* 16:253–257.
- BABA, K. & I. HAMATANI. 1952. Observations on the spawning habits of some of the Japanese Opisthobranchia (1). *Publications of the Seto Marine Biological Laboratory* 2:87–90.
- BABA, K. & I. HAMATANI. 1970. The anatomy of *Ercolania boodleeae* (Baba, 1938) from Seto, Kii, Middle Japan (Opisthobranchia: Sacoglossa). *Publications of the Seto Marine Biological Laboratory* 18:215–222.
- BEEMAN, R. D. & G. C. WILLIAMS. 1980. Opisthobranchia and Pulmonata: the sea slugs and allies. Pp. 308–354 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, California.
- BEHRENS, D. W. 1980. A review of the literature on the opisthobranch fauna of San Francisco Bay. *Opisthobranch Newsletter* 12:34–37.
- BEHRENS, D. W. 1991a. Pacific Coast Nudibranchs, A Guide to the Opisthobranchs, Alaska to Baja California, 2nd ed. *Sea Challengers: Monterey*. 107 pp.
- BEHRENS, D. W. 1991b. Pacific Coast Nudibranchs: Supplement 1. Radula. *Sea Challengers: Monterey*. 11 pp.
- BEHRENS, D. W. 1998. Reader forum: Locality data; *Placida dendritica* (Alder & Hancock, 1843). *Opisthobranch Newsletter* 24:41.
- BEHRENS, D. W. & M. TUEL. 1977. Notes on the Opisthobranch fauna of South San Francisco Bay. *The Veliger* 20:33–36.
- BELICK, F. P. 1975. Additional opisthobranch mollusks from Oregon. *The Veliger* 17:276–277.
- BERGH, VON R. 1894. XIII. Die Opisthobranchien. *Bulletin of the Museum of Comparative Zoology* 25:191–225.
- BERTSCH, H. 1971. Natural history and occurrence of opisthobranchs of Las Cruces, Baja California, Mexico, and vicinity. *The Echo* 3:16.
- BERTSCH, H. 1973. Distribution and natural history of opisthobranch gastropods from Las Cruces, Baja California del Sur, Mexico. *The Veliger* 16:105–111.
- BERTSCH, H. & A. A. SMITH. 1973. Observations on three opisthobranchs (Mollusca: Gastropoda) of the La Paz area, Baja California, Mexico. *Southwestern Naturalist* 18:165–176.
- BERTSCH, H., M. D. MILLER & A. GRANT. 1998. Notes on opisthobranch community structures at Bahía de los Angeles, Baja California, Mexico (June 1998). *Opisthobranch Newsletter* 24:35–36.
- BLEAKNEY, J. S. 1989. Morphological variation in the radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) from Atlantic and Pacific populations. *The Veliger* 32:171–181.
- BLEAKNEY, J. S. 1990. Indirect evidence of a morphological response in the radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) to different algal prey. *The Veliger* 33:111–115.
- BLEAKNEY, J. S. 1996. Sea Slugs of Atlantic Canada and the Gulf of Maine. Nimbus Publishing and the Nova Scotia Museum: Halifax. 216 pp.
- BURN, R. 1998. Order Sacoglossa. Pp. 961–974 in P. L. Beesley, G. J. B. Ross & A. Wells (eds.), *Mollusca, the Southern Synthesis, Part B. Fauna of Australia Vol. 5*. CSIRO Publishing: Melbourne.
- CASE, R. M. 1972. An ecological study of *Stiliger fuscovittata* (Mollusca: Opisthobranchia). M.A. Thesis, San Francisco State University. 76 pp.
- CHAPMAN, J. W. & J. T. CARLTON. 1991. A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 11:386–400.
- CHIA, F.-S. 1971. Oviposition, fecundity, and larval development of three sacoglossan opisthobranchs from the Northumberland coast, England. *The Veliger* 13:319–325.
- CHIA, F.-S. & M. SKEEL. 1973. The effect of food consumption on growth, fecundity, and mortality in a sacoglossan opisthobranch, *Olea hansineensis*. *The Veliger* 16:153–158.
- CIMINO, G. & M. T. GHISELIN. 1998. Chemical defense and evolution in the Sacoglossa (Mollusca: Gastropoda: Opisthobranchia). *Chemoecology* 8:51–60.
- CIMINO, G., A. FONTANA, & M. GAVAGNIN. 1999. Marine opisthobranch molluscs: Chemistry and ecology in sacoglossans and dorids. *Current Organic Chemistry* 3:327–372.
- CLARK, K. B. 1975. Nudibranch life cycles in the Northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer wissenschaftliche Meeresuntersuchungen* 27:28–69.
- CLARK, K. B. 1992. Plant-like animals and animal-like plants: Symbiotic coevolution of ascoglossan (=sacoglossan) molluscs, their algal prey, and algal plastids. Pp. 515–530 in *Algae and Symbioses*. Biopress Limited: Bristol.
- CLARK, K. B. 1994. Ascoglossan (=sacoglossan) molluscs in the Florida Keys: rare marine invertebrates at special risk. *Bulletin of Marine Science* 54:900–916.
- CLARK, K. B. 1995. Rheophilic/oligotrophic lagoonal communities: through the eyes of slugs (Mollusca: Opisthobranchia). *Bulletin of Marine Science* 57:242–251.
- CLARK, K. B. 1997. Reader forum: Range extension vs. new record. *Opisthobranch Newsletter* 23:17–18.
- CLARK, K. B. & M. BUSACCA. 1978. Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion of the extent of chloroplast symbiosis and the evolution of the order. *Journal of Molluscan Studies* 44:272–282.
- CLARK, K. B. & D. DEFRESE. 1987. Population ecology of Ca-

- ribbean Ascoglossa (Mollusca: Opisthobranchia): a study of specialized algal herbivores. *American Malacological Bulletin* 5:259–280.
- CLARK, K. B. & D. R. FRANZ. 1969. Occurrence of the sacoglossan opisthobranch *Hermaea dendritica* Alder & Hancock in New England. *The Veliger* 12:174–175.
- CLARK, K. B. & A. GOETZFRIED. 1978. Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies* 44:283–294.
- CLARK, K. B. & K. R. JENSEN. 1981. A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *International Journal of Invertebrate Reproduction* 3:57–64.
- CLARK, K. B., K. R. JENSEN & H. M. STIRTS. 1990. Survey for functional kleptoplasty among west Atlantic Ascoglossa (= Sacoglossa) (Mollusca: Opisthobranchia). *The Veliger* 33:339–345.
- COCKERELL, T. D. A. & C. ELIOT. 1905. Notes on a collection of Californian nudibranchs. *Journal of Malacology* 12:31–53.
- CRANE, S. 1971. The feeding and reproductive behavior of the sacoglossan gastropod *Olea hansineensis* Agersborg, 1923. *The Veliger* 14:57–59.
- DEBELIUS, H. 1996. Nudibranchs and Sea Snails. Indo-Pacific Field Guide. IKAN-Unterwasserarchiv: Frankfurt. 321 pp.
- DEN HARTOG, C. 1959. Distribution and ecology of the slugs *Alderia modesta* and *Limapontia depressa* in the Netherlands. *Beaufortia* 7:15–36.
- DI MARZO, V., A. MARIN, R. R. VARDARO, L. DE PETROCELLI, G. VILLANI & G. CIMINO. 1993. Histological and biochemical bases of defense mechanisms in four species of Polybranchioidea ascoglossan molluscs. *Marine Biology* 117:367–380.
- DOTY, M. S. & G. AGUILAR-SANTOS. 1970. Transfer of toxic algal substances in marine food chains. *Pacific Science* 24:351–355.
- DUSHANE, H. & G. G. SPHON. 1968. A checklist of intertidal mollusks for Bahía Willard and the southwestern portion of Bahía San Luis Gonzaga, State of Baja California, Mexico. *The Veliger* 10:233–246.
- ELLIS, W. 1999. *Stiliger fuscatus*. Australasian Nudibranch News 2:4.
- ELLIS, W. 2000. *Ercolania* sp. Australasian Nudibranch News 2:20.
- FARMER, W. M. 1967. Notes on the opisthobranchia of Baja California, Mexico, with range extensions—II. *The Veliger* 9:340–342.
- FARMER, W. M. 1980. Sea-Slug Gastropods. W. M. Farmer Enterprises: Tempe. 177 pp.
- FARMER, W. M. 1996. Personal notes: From Wes Farmer. *Opisthobranch Newsletter* 22:15.
- FERREIRA, A. J. & H. BERTSCH. 1975. Anatomical and distributional observations of some opisthobranchs from the Panamic faunal province. *The Veliger* 17:323–330.
- FOSTER, N. R. 1987. *Hermaea vancoverensis* O'Donoghue, 1924, from Kodiak Island and Unga Island, Alaska. *The Veliger* 30:98.
- FOX, L. R. & P. A. MORROW. 1981. Specialization: species property or local phenomenon? *Science* 211:887–893.
- FRETTER, V. 1941. On the structure of the gut of the Ascoglossan nudibranchs. *Proceedings of the Zoological Society of London. Series B* 110:185–198.
- GASCOIGNE, T. 1975. The radula and reproductive system of *Olea hansineensis* Agersborg, 1923 (Gastropoda: Opisthobranchia: Sacoglossa). *The Veliger* 17:313–317.
- GASCOIGNE, T. 1978. The internal anatomy of *Stiliger fuscatus* (A. Gould, 1870) (Opisthobranchia: Sacoglossa). *Zoological Journal of the Linnean Society* 63:265–274.
- GASCOIGNE, T. 1985. A provisional classification of families of the order Ascoglossa (Gastropoda: Nudibranchiata). *Journal of Molluscan Studies* 51:8–22.
- GELLER, J. B., E. D. WALTON, E. D. GROSHOLZ, & G. M. RUIZ. 1997. Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. *Molecular Ecology* 6:901–906.
- GODDARD, J. 1973. Opisthobranchs of San Francisco Bay. *Tabulata* 6:8–10.
- GODDARD, J. H. R. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. *The Veliger* 27:143–163.
- GODDARD, J. H. R. 1987. Observations on the opisthobranch mollusks of Punta Gorda, California, with notes on the distribution and biology of *Crimora coneja*. *The Veliger* 29:267–273.
- GODDARD, J. H. R. 1990. Additional opisthobranch mollusks from Oregon, with a review of deep-water records and observations on the fauna of the south coast. *The Veliger* 33:230–237.
- GODDARD, J. H. R., T. A. WAYNE & K. R. WAYNE. 1997. Opisthobranch mollusks and the pulmonate limpet *Trimusculus reticulatus* (Sowerby, 1835) from the Outer Washington coast. *The Veliger* 40:292–297.
- GONOR, J. J. 1961. Observations on the biology of *Hermaea smithi*, a sacoglossan opisthobranch from the west coast of North America. *The Veliger* 4:85–98.
- GOSLINER, T. 1987. Nudibranchs of Southern Africa. A Guide to Opisthobranch Molluscs of Southern Africa. *Sea Challengers: Monterey*. 136 pp.
- GOSLINER, T. M. 1995. The genus *Thuridilla* (Opisthobranchia: Elysiidae) from the tropical Indo-Pacific, with a revision of the phylogeny and systematics of the Elysiidae. *Proceedings of the California Academy of Sciences* 49:1–54.
- GOSLINER, T. M. & G. C. WILLIAMS. 1970. The opisthobranch mollusks of Marin County, California (Gastropoda). *The Veliger* 13:175–180.
- GOSLINER, T. M. & G. C. WILLIAMS. 1973. Additions to the opisthobranch mollusk fauna of Marin County, California, with notes on their natural history. *The Veliger* 15:352–354.
- GOSLINER, T. M., D. W. BEHRENS & G. C. WILLIAMS. 1996. Coral Reef Animals of the Indo-Pacific: Animal Life from Africa to Hawai'i Exclusive of the Vertebrates. *Sea Challengers: Monterey*. 314 pp.
- GRAVES, D. A., M. A. GIBSON & J. S. BLEAKNEY. 1979. The digestive diverticula of *Alderia modesta* and *Elysia chlorotica* (Opisthobranchia: Sacoglossa). *The Veliger* 21:415–422.
- GREENE, R. W. 1968. The egg masses and veligers of southern California sacoglossan opisthobranchs. *The Veliger* 11:100–104.
- GREENE, R. W. 1970a. Symbiosis in sacoglossan opisthobranchs: symbiosis with algal chloroplasts. *Malacologia* 10:357–368.
- GREENE, R. W. 1970b. Symbiosis in sacoglossan opisthobranchs: translocation of photosynthetic products from chloroplast to host tissue. *Malacologia* 10:369–378.
- GREENE, R. W. 1970c. Symbiosis in sacoglossan opisthobranchs: functional capacity of symbiotic chloroplasts. *Marine Biology* 7:138–142.
- GREENE, R. W. & L. MUSCATINE. 1972. Symbiosis in sacoglossan opisthobranchs: photosynthetic products of animal-chloroplast associations. *Marine Biology* 14:253–259.
- HADFIELD, M. G. & M. SWITZER-DUNLAP. 1984. Opisthobranchs. Pp. 209–350 in A. S. Tompa, N. H. Verdonk & J. A. M. van den Biggelaar (eds.), *The Mollusca, Reproduction*. Volume 7. Academic Press: New York.
- HAND, C. 1955. *Alderia modesta* in Washington. *The Nautilus* 69:72.
- HAND, C. & J. STEINBERG. 1955. On the occurrence of the nu-

- dibranch *Alderia modesta* (Lovén, 1844) on the central Californian coast. *The Nautilus* 69:22–28.
- HARTMAN, M. J. & R. G. ZAHARY. 1983. Biogeography of protected rocky intertidal communities of the northeastern Pacific. *Bulletin of Marine Science* 33:729–735.
- HAVENHAND, J. N. 1991. On the behavior of opisthobranch larvae. *Journal of Molluscan Studies* 57:119–131.
- HAWKINS, S. J. & R. G. HARTNOLL. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review* 21:195–282.
- HURST, A. 1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. *The Veliger* 9:255–288.
- ICHIKAWA, M. 1993. Saccoglossa (Opisthobranchia) from the Ryukyu Islands. *Publications of the Seto Marine Lab* 36:119–139.
- IRELAND, C. & J. FAULKNER. 1981. The metabolites of the marine molluscs *Tridachella diomedea* and *Tridachia crispata*. *Tetrahedron* 37, supplement 1:233–240.
- IRELAND, C., D. J. FAULKNER, B. A. SOLHEIM & J. CLARDY. 1978. Tridachione, a propionate-derived metabolite of the opisthobranch mollusc *Tridachella diomedea*. *Journal of the American Chemical Society* 100:1002–1003.
- JAECKLE, W. B. 1984. The opisthobranch mollusks of Humboldt County, California. *The Veliger* 26:207–213.
- JENSEN, K. R. 1980. A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. *Malacological Review* 13:55–77.
- JENSEN, K. R. 1982. Chemoreception as a factor in food location of *Elysia cauze* Marcus (Opisthobranchia, Ascoglossa). *Marine Behaviour and Physiology* 8:205–218.
- JENSEN, K. R. 1983. Factors affecting feeding selectivity in herbivorous Ascoglossa (Mollusca: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology* 66:135–148.
- JENSEN, K. R. 1988. Chemoreception in six species of Florida Ascoglossa (Mollusca: Opisthobranchia), a comparative study of responses to homogenates of food and non-food plants. *Ophelia* 28:231–242.
- JENSEN, K. R. 1991. Review of the usage of the synonyms Saccoglossa Ihering, 1876 and Ascoglossa Bergh, 1876. *Proceedings of the Tenth International Malacological Congress (Tübingen 1989)* 541–544.
- JENSEN, K. R. 1993. Morphological adaptations and plasticity of radular teeth of the Sacoglossa (=Ascoglossa) (Mollusca: Opisthobranchia) in relation to their food plants. *Biological Journal of the Linnean Society* 48:135–155.
- JENSEN, K. R. 1996. Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). *Philosophical Transactions of the Royal Society of London, B* 351:91–122.
- JENSEN, K. R. 1997. Evolution of the Sacoglossa (Mollusca, Opisthobranchia) and the ecological associations of their food plants. *Evolutionary Ecology* 11:301–335.
- JENSEN, K. & K. B. CLARK. 1983. Annotated checklist of Florida ascoglossan opisthobranchia. *The Nautilus* 97:1–13.
- KAY, E. A. 1964. A new species of *Berthelinia* and its associated sacoglossans in the Hawaiian Islands. *Proceedings of the Malacological Society of London* 36:191–197.
- KEEN, A. M. 1971. Sea Shells of Tropical West America, Marine Mollusks from Baja California to Peru. 2nd ed. Stanford University Press: Stanford, California. 1064 pp.
- KEEN, A. M. 1973. Some nomenclatural problems in Sacoglossa. *The Veliger* 16:238.
- KEEN, A. M. & A. G. SMITH. 1961. West American species of the bivalved gastropod genus *Berthelinia*. *Proceedings of the California Academy of Science, Fourth Series* 30:47–66.
- KNOWLTON, N. 1993. Sibling species in the sea. *Annual Reviews of Ecology and Systematics* 24:189–216.
- KRESS, A. 1971. Über die Entwicklung der Eikapselvolumina bei verschiedenen Opisthobranchier-Arten (Mollusca, Gastropoda). *Helgoländer wissenschaftliche Meeresuntersuchungen* 22:326–349.
- KRUG, P. J. 1998a. Chemical and larval ecology of opisthobranch molluscs: variable development modes and settlement cues for larvae of *Alderia modesta*. Ph.D. Dissertation, University of California, San Diego. 227 pp.
- KRUG, P. J. 1998b. Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the ascoglossan *Alderia modesta*. *Marine Biology* 132:483–494.
- KRUG, P. J. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Marine Ecology Progress Series* 213:177–192.
- KRUG, P. J. & A. E. MANZI. 1999. Waterborne and surface-associated carbohydrates as settlement cues for larvae of the specialist marine herbivore *Alderia modesta*. *Biological Bulletin* 197:94–103.
- KRUG, P. J. & R. K. ZIMMER. 2000. Developmental dimorphism and expression of chemosensory-mediated behavior: habitat selection by a specialist marine herbivore. *Journal of Experimental Biology* 203:1741–1754.
- KRUG, P. J. & R. K. ZIMMER. 2000b. Larval settlement: chemical markers for tracing production, transport, and distribution of a waterborne cue. *Marine Ecology Progress Series* 207:283–296.
- LAMBERT, P. 1976. Records and range extensions of some north-eastern Pacific opisthobranchs (Mollusca: Gastropoda). *Canadian Journal of Zoology* 54:293–300.
- LANCE, J. R. 1961. A distributional list of southern California opisthobranchs. *The Veliger* 4:64–69.
- LANCE, J. R. 1962. A new *Stiliger* and a new *Corambella* (Mollusca: Opisthobranchia) from the northwestern Pacific. *The Veliger* 5:33–38.
- LANCE, J. R. 1966. New distributional records of some north-eastern Pacific Opisthobranchiata (Mollusca: Gastropoda) with descriptions of two new species. *The Veliger* 9:69–81.
- LANCE, J. R. 1996. Field notes: *Alderia modesta*. *Opisthobranch Newsletter* 22:35.
- LANCE, J. R. 1997. Reader forum: potential prey of *Roboastra tigris*. *Opisthobranch Newsletter* 23:29–30.
- LANCE, J. R. 1998. Reader forum: from James R. Lance. *Opisthobranch Newsletter* 24:2.
- LARSON, M. & H. BERTSCH. 1974. Northward range extensions for *Lobiger souverbii* (Opisthobranchia: Sacoglossa) in the eastern Pacific. *The Veliger* 17:225.
- LEE, R. S. & P. BROPHY. 1969. Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. *The Veliger* 12:220–221.
- LEE, R. S. & N. R. FOSTER. 1985. A distributional list with range extensions of the opisthobranch gastropods of Alaska. *The Veliger* 27:440–448.
- LEWIN, R. A. 1970. Toxin secretion and tail autotomy by irritated *Oxynoe panamensis* (Opisthobranchiata; Sacoglossa). *Pacific Science* 24:356–358.
- LONG, S. J. 1969. Records of *Trinchesia virens*, *Trinchesia fulgens*, and *Placida dendritica* from San Luis Obispo County, California. *Tabulata* 2:9–12.
- MACFARLAND, F. M. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. *Proceedings of the California Academy of Sciences, Fourth Series* 13:389–420.
- MACFARLAND, F. M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. *Memoirs of the California Academy of Sciences* 6:1–546.
- MARCUS, E. 1961. Opisthobranch mollusks from California. *The Veliger* 3 (Suppl.):1–84.